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The Impact of Malaria on Birds in Hawaii Volcanoes National Park

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INTRODUCTION

The Hawaiian Islands are the most isolated land mass in the world, lying in the middle of the Pacific Ocean over 4,500 km from North America and 5,000 km from Asia. Because of their sterile volcanic origin and great distances from the continents, colonization was infrequent, but when it did occur, the organisms, isolated from mainland influences and constraints, underwent rapid and extensive adaptive radiation. Among the most spectacular examples are the land birds, in which 10 of the 11 families have endemic species. Unfortunately, more of these endemic species have become extinct than in any other comparable region of the world. There have been many proposed hypotheses as to why so many native bird species succumbed in the short time period following discovery of the Islands by Captain Cook in 1778; these include habitat destruction by man and introduced ungulates, indiscriminate collecting of birds, competition with introduced birds, introduced predators, and introduced diseases. In this paper we will attempt to ascertain the role that the introduced malaria parasite has played in the decline of Hawaiian avifauna.

Much concern has been expressed over the relationship between introduced diseases and the depletion of the native Hawaiian birds, but the many papers addressing this problem have been little more than technical criticisms and have not re-examined the underlying hypothesis. Warner's (1968) study of the presumed role that introduced malaria and avian pox played in the extinction of the native Hawaiian birds is the only major published work dealing with this subject. He proposed that an "imaginary line" existed at approximately 600 m, above which there were no mosquitoes and below which native birds were not found, presumably because they had succumbed to introduced diseases. His findings have found wide

acceptance as an example of disease limiting a host population; this despite the fact that occasional observations appear not to demonstrate the validity of Warner's arguments. In fact, Berger (1975) in his review of this subject writes:

> "This is meager evidence, indeed, for the numerous assertions in the literature that the extinction of so many native forest birds was due to introduced bird diseases. It may have been so, but no trustworthy evidence has been published as of 1974."

In this study we examine the species of avian malaria that are present today in the Hawaiian Islands, the susceptibility of extant bird species to the malaria parasite, the overall percentage of wild birds infected with malaria, distributional patterns of potential vectors, sporogonic development in the vectors, and the epizootiology of malaria in the Hawaiian Islands. We will then present kinds of evidence which show that the avian disease problem in Hawaii is much more complex than originally proposed by Warner (1968). We shall also document that malaria probably did not have a major impact upon reducing the numbers of Hawaiian birds in the late 19th century, but is presently restricting populations and affecting distributional and behavioral patterns of the native birds. Finally, management recommendations will be suggested to minimize the present obvious problem and assure continued healthy avian populations.

METHODS

Study Areas

Study areas consisted of 16 stations along two transects, established at approximately 300 m intervals on the southern and eastern slopes of Mauna Loa Volcano, Hawaii (Fig. 1). The southern transect spanned principally xeric forest habitat, while the eastern transect crossed mesic forests. The dry forest was characterized by introduced tree species such as koa haole (Leucacena leucocephala L.), Christmas berry (Schinus terebinthifolius Raddi) and guava (Psidium guajava L.) at lower elevations, ohia (Metrosideros collina Forst.) with scattered mamane (Sophora chrysophylla Salisb.) throughout the mid-elevation range, and predominantly mamane in the higher parts. The wet forest habitat was composed of scattered ohia and numerous introduced tree species near sea level, a mixed koa (Acacia koa Gray)-ohia forest in the mid-elevational ranges, and scrub ohia at the upper elevations. A more detailed analysis of these vegetation types may be found in Mueller-Dombois and Fosberg (1974).

Field Techniques

From 1978-1979 wild birds were mist-netted bimonthly at each station, while at 1200 m elevation they were netted monthly over a three-year period (1978-1980). Each bird was bled by clipping a toe nail, a thin blood smear was taken, and the slide fixed for 30 sec in absolute methyl alcohol; before release the bird was measured and banded with unique combinations of colors, and a single USFWS metal band.

During August 1978, four malaria-naive Laysan Finch (Psittirostra cantans) were set out at each station for a 12-day period. Two birds were

placed in open bamboo cages within the canopy, approximately 8 m above the ground, while two controls were placed in an adjacent cage wrapped in mosquito-proof netting. Following the exposure period all birds were returned to the laboratory and monitored for three weeks.

At each station artificial mosquito oviposition sites were maintained with a constant supply of water. All sites were checked for eggs, larvae, and pupae each month during 1978-1979. At each station potential natural oviposition sites were identified and examined regularly for larval activity. Counts of adult mosquitoes from a series of 30 light traps run 24 hours a day by the Hawaii Department of Health were supplemented by monthly trapping at each of the 16 study stations using Standard New Jersey Mosquito Light Traps. Biting collections were taken on a monthly basis for both Culex quinquefasciatus and Aedes albopictus; additional biting collections for C. quinquefasciatus were made by a number of volunteers at selected stations (Goff and van Riper 1980).

Laboratory Techniques

Strains of malaria were established from wild caught and moribund Hawaiian forest birds. The original strain (H-1) was collected from an Apapane found at 1200 m elevation, and subsequent strains were established from a Japanese White-eye (W-1), a House Sparrow (S-1), and another Apapane (H-2). Each strain was maintained through subinnoculations of infected blood into canaries, a standard method employed in Plasmodium research (Garnham 1966).

Ten each of Apapane (Himatione sanguinea), Iiwi (Vestiaria coccinea), Japanese White-eye (Zosterops japonica), Red-billed Leiothrix (Leiothrix lutea), and Amakihi (Loxops virens) were collected from high altitude forest habitats on Mauna Loa and transported in mosquito-proof cages to

the Avian Disease Laboratory at the Hawaii Field Research Center. In addition 15 Amakihi were also taken from the dry forest of Mauna Kea where malaria is apparently absent (van Riper 1975). These population samples were made to see if a differential resistance to the malaria parasite has developed in subpopulations of a host. Forty Laysan Finches were captured on the mosquito-free Laysan Island and transported by boat in mosquito-proof cages to Hawaii island. All birds were allowed a closely monitored acclimation period, during which time they were fed food ad libitum and body weights taken every second day. During this treatment period, blood smears were taken on a regular basis and searched for the presence of haematozoan infections. To ensure that no birds had infections that were not detected by microscopy, blood was extracted from selected individuals and subinnoculated back to canaries, a technique that has been shown to reveal latent infections (Herman et al. 1966). After weight stabilization, all birds were treated with Solumet and Tramasol in order to clear them of helminth endoparasites and coccidia.

Following the parasite-clearing process, five captive Apapane, Iiwi, Red-billed Leiothrix, Japanese White-eye, Laysan Finch, Mauna Loa Amakihi, and six Mauna Kea Amakihi, were innoculated intramuscularly with 0.1 cc of infected blood. Each species group was challenged within a 2-day period with blood from the same canary host. After day 4 each bird was bled at regular intervals until the host succumbed or parasitemia levels fell to a chronic state. Throughout the entire challenge period physical conditions were monitored daily. Five other individuals of each group composed controls which were maintained in mosquito-proof cages and monitored throughout the experiment. In addition, periodicity was examined during peak levels of parasitemia in the Canary, Apapane, and Amakihi, of which the former two were bled every 4 hours over two 24-hour periods.

Blood slides were treated for 30 min with Giemsa stain in a solution buffered with Na_2PO_4 and KH_2PO_4 to a pH of 7.17. Each slide was read under oil immersion at 1000X for 10 min, or until a minimum of 25,000 red blood cells (RBC) had been examined. All parasites were classed as either gametocytes, schizonts, or trophozoites. In the case of heavy infections, 100 parasites were counted and categorized. The average number of RBC per field was recorded for each slide as was the mean number of fields read/min by the observer. The number of cells examined on each slide (Ce) was determined using the following formula:

$$Ce = (B_f)\ (F_m)\ (M_r)$$

where B_f = number of RBC per field; F_m = fields per min read; and M_r = min slide was read. The formula used to determine the number of parasites/10,000 RBC was:

$$\text{Parasites/10,000 RBC} = (P_o)\quad \frac{10,000}{Ce}$$

where P_o = number of parasites observed.

To take into account the refractory ability of a bird species against the malarial parasite, and the ability of that host to survive once infected, the following formula was developed for an Index of Adaptation (I_a):

$$I_a = \frac{(\alpha + \beta)}{2n}$$

where α = number of individuals surviving the challenge; β = number of refractory individuals, and n = sample size of the challenge group. In this manner, species lacking any immunogenetic capacity would have an I_a = 0. The closer I_a approached 1, the greater the ability of the host group to survive the disease.

Colonies of C. quinquefasciatus were established in the laboratory from larvae collected in the wild. Newly emerged adults were removed to biting cages and maintained on a sugar and water combination. From four to six days after emergence, females were offered blood meals from infected birds, and following engorgement were removed to separate cages. Ookinetes were searched for in mosquito stomach blood at 12-24 hours after engorgement using diluted smears, fixed in methyl alcohol and stained with Giemsa; stomachs were examined for oocysts via wet mounts and salivary glands were stained with Giemsa to show any sporozites, following the technique outlined in Garnham (1966). Females previously engorged on infected birds were placed in biting cages with noninfected birds to complete laboratory transmission.

Daily activity cycles of C. quinquefasciatus and A. albopictus were determined in the laboratory. Three recently emerged females of each species were placed in sealed glass jars containing water plus sugar and were allowed to acclimate for three days. The jars were maintained at ambient temperature with humidity at 100%, and sealed to eliminate problems with air movement and CO_2 attraction. During the first 10 min of each hour over a 24 hr period, the total number of seconds any one of the three experimental mosquitoes were flying was recorded. Four replications were made on each species. During the dark hours low-intensity light filters were used so as not to attract the mosquitoes.

All statistical analyses were computed on a Burroughs 6700 using SPSS programs (Nie et al. 1975). Where data were not normally distributed, transformations were used before application of statistical tests. The level of statistical significance was considered to be 0.05.

RESULTS

Field Results

In 14,027 net hours from 1977-1979, 2,702 birds were captured and bled. All of the 16 study locations were sampled with similar effort, resulting in a mean of 935 net hours/station; however, the number of birds and species captured at each location varied. The only malaria parasite found during this study was Plasmodium relictum ssp. capistranoae Russell (Laird and van Riper, in press). Microfilaria, babesoids, and trypanosomes were not detected, and appear to be absent in the birds on Hawaii. However, Atoxoplasma sp. was identified in blood smears from the House Sparrow, Spotted Munia, and Japanese White-eye, this being the first record of the parasite in the Hawaiian Islands. Results of this discovery are discussed in a separate paper (van Riper et al., in prep.).

Of the 2,702 blood slides taken from wild birds, 2,365 were of the native Apapane, Amakihi, Iiwi, Elepaio (Chasiempis sandwicenses), Hawaiian Thrush, and introduced House Finch (Carpodacus mexicanus), House Sparrow (Passer domesticus), Spotted Munia (Lonchura punctulata), American Cardinal (Cardinalis cardinalis), Japanese White-eye, and Red-billed Leiothrix. Eighteen species were captured and bled during the course of this study, but we will, for the most part, deal in this paper only with the above mentioned passerine birds because of the small sample sizes of the other seven species (see Appendix I).

The total number of birds captured/100 net hours showed highs in March-June and September-October with lows in November-February and July-August (Table 1). The July-August decrease was attributable to the low numbers of Japanese White-eyes captured during that two-month period. Decreases in native bird densities did not usually occur until later in

the year. There was a difference between the numbers and distribution patterns of native and introduced birds captured at each station, especially in mesic areas (Fig. 2). Greatest introduced bird densities occurred in the lowland mesic habitat, and generally decreased in abundance with higher elevation. Native species were absent in mesic forest below 1,000 m, after which their numbers increased with elevation. Introduced birds were more uniformly distributed throughout all elevational ranges of the xeric habitat, while native birds ranged lower in the xeric forest (when compared to their distribution in mesic habitat), and reached their highest densities above 1,500 m.

Infection Rates -- Of the 2,365 wild birds analyzed for blood parasites during this study, 7.8% were infected with malaria. The native Apapane population had the highest percentage of infected individuals (Fig. 3); the introduced House Finch and House Sparrow populations also had high percentages, albeit they were three times lower than that of the Apapane. The greatest percentage of individuals from the avian community infected with malaria occurred during November and December (Table 2). Most native species had increases in the percentage of infected individuals in their respective populations sometime during the months of July to December (Fig. 4), indicating that during this time of the year native birds were most likely to be exposed to the malaria parasite. On the other hand, the introduced species tended to have a more uniform number of infected birds throughout the annual cycle, and in those species which did have peaks, a yearly pattern was not evident.

Avian populations from the mesic and xeric forests of Mauna Loa had significantly different levels of malaria infection in each habitat type (Table 3: $\chi^2_c = 11.24$; df = 1; $P < 0.001$). The wet forest consistently

supported higher malaria levels, which was probably related to the increased availability of vector breeding sites. Elevation, however, appeared to have the greatest influence upon population infection rates on Mauna Loa (Fig. 5). This suggests that elevation is tied more closely to malaria infection levels than is either the time of year or the forest type.

There was no significant difference between the number of young and adults which were infected with malaria in either the native (χ^2_c = 0.0; df = 1; $\underline{P}$ = 1.0) or introduced species (χ^2_c = 0.49; df = 1; $\underline{P}$ = 0.48), which indicates that young birds are not being infected preferentially, as shown by Blackmore and Dow (1958) in North America. Furthermore, a recaptured bird was not more likely to have malaria than was a first capture (χ^2_c = 2.93; df = 1; $\underline{P}$ = 0.09). Birds that had one, two or more than two visible lesions either on their feet, legs, or face were more likely to have malaria than were individuals without lesions (χ^2 = 127.9; df = 3; $\underline{P}$ < 0.001). If the lesions were associated with diseases carried by airborne vectors (such as avian pox), birds with lesions perhaps would have been exposed to mosquitoes and thereby have had a greater chance of exposure to the malaria parasite. These data do not support McGhee's (1970) hypothesis that avian viruses may simulate immune and autoimmune effects within the host toward the malaria parasite.

Birds which were collected moribund or that were killed by automobiles had higher incidences of malaria than did birds captured in mist-nets. Perhaps the malaria parasite debilitates a bird so that diseased individuals are more likely to be struck by cars. However, birds accidentally killed in mist-nets were not more likely to have malaria than were normally processed birds. Low, medium and high fat levels in a bird

had no relationship to malaria infections ($\chi^2 = 3.81$; df = 3; $\underline{P} = 0.28$), nor did degree of molt ($\chi^2 = 1.75$; df = 3; $\underline{P} = 0.63$).

Parasitemia Levels -- The overall parasitemia level from the entire avian community on Mauna Loa was 2.3 parasites/10,000 RBC. The heaviest parasitemia levels occurred in September-October (Table 3), and did not exhibit the July-August decrease as did the percent of infected birds. As well as having the greatest percentage of infected individuals, the Apapane also had the highest overall parasitemia levels throughout the year on Mauna Loa (Fig. 4). In every month native birds had higher parasitemia levels than did the introduced species, indicating the extreme susceptibility of the endemic avifauna. Introduced species had low numbers of parasites/10,000 RBC throughout the year, indicating primarily latent infections. There was a significant difference in overall parasitemia levels between the bird species on Mauna Loa (analysis of variance: df = 10, $\underline{P} < 0.001$).

Elevation had a marked influence on parasitemia levels in the birds on Mauna Loa (Fig. 5). The highest parasitemia levels were between 900-1,500 m elevation, that area where native bird and breeding mosquito distributions overlapped. Additionally, birds had higher parasitemia levels at lower elevations in the xeric than in the mesic habitats, which is most likely a function of native species being found at lower elevations in the drier areas (see Fig. 2). The low parasitemia levels at higher elevations is probably a factor of decreased vector abundance.

The principal breeding period of the native Hawaiian birds is December to May (Baldwin 1953; Berger 1981; Conant 1977; Eddinger 1970; van Riper 1978, 1980, van Riper and Scott 1979), and this was the time of year when we found the lowest parasitemia levels. Degree of molt, in

combination with cloacal protuberance or brood patch was used as an index to measure the effect of breeding on malaria parasite levels in the birds. We found no significant difference in parasitemia levels between the breeding and non-breeding periods using these parameters ($\chi^2 = 1.75$; df = 3; $P = 0.63$). Successive captures were made throughout the year on a number of individually color-marked birds, and those individuals with chronic malaria infections did not exhibit any increase in parasitemia levels during the breeding season, and were also successful in fledging young. This indicates that an increase in reproductive hormones presently has little noticeable gross effect upon the malaria cycle in native Hawaiian birds. While young were not more likely to have malaria than were older birds, levels of parasitemia were up to six times greater in first-year birds, particularly the native species. This implies that younger birds have less resistance to the malaria parasite once contracted.

Vector Distributions -- Because of the porosity of the volcanic substrate in Hawaii, which results in a patchy distribution of potential breeding sites, mosquito distribution was not uniform over the entire altitudinal range of the forests on Mauna Loa (see also discussion by Goff and van Riper, 1980). Greatest mosquito densities were found to be associated with kipukas (an island of older vegetation surrounded by a more recent lava flow with younger vegetation) and human habitation (most drinking water in Hawaii is in water tanks which store rainfall from house roofs). Two mosquito species were collected regularly throughout this study, Aedes albopictus and Culex quinquefasciatus.

Larvae and pupae of C. quinquefasciatus were present from sea level to 1500 m elevation throughout each month of this study (Fig. 6). During

July-August this mosquito was found breeding up to 1650 m elevation, the highest reaches of the extant mesic forests of Mauna Loa. In addition to these data from our artificial oviposition sites, "natural" oviposition sites were found to be pools of water on nonporous lava and felled trees, treeholes, ground pools, hapu'u stumps, pig wallows, rain barrels, and cattle watering troughs. Goff and van Riper (1980) documented breeding of C. quinquefasciatus throughout the entire year at elevations of 1350 m in xeric habitat and 1500 m in mesic habitat on Mauna Loa. Other records from the island of Hawaii record breeding at even higher elevations. Swezey and Williams (1932) found egg rafts in a rain barrel at 1829 m on Mt. Hualalai and larvae at 1981 m on Mauna Kea, and Komatsu (1966) reported egg rafts from concrete pools at 1981 m on Mauna Kea.

Adult C. quinquefasciatus were collected in light traps operated by the Hawaii State Department of Health at elevations below 900 m. This mosquito showed increasing adult populations from January until July-August, after which numbers fell precipitously (Fig. 7). Standard New Jersey Mosquito Light traps were operated at all stations above 600 m for a six-month period, but no mosquitoes were collected, even when a CO_2 attractant was employed. These data point to the generally overall low density of mosquitoes at higher elevations on Hawaii. During this same time period biting collections using humans at all stations above 300 m elevation yielded negative results for C. quinquefasciatus. For example, during three 24-hr biting collections at 1200 m elevation, only two adult mosquitoes were observed and neither alighted. Even though adult C. quinquefasciatus reach high levels at lower elevations during the warmer months of the year, densities at the higher elevations are apparently quite low, albeit they are still in great enough numbers to cause high levels of avian malaria.

A. albopictus larvae and pupae were recovered from our artificial oviposition sites only up to 200 m for all months of the study. Other oviposition sites were associated with human activity and consisted primarily of construction equipment, discarded bottles, tires, cans and sundry human refuse. No A. albopictus larvae were found above 900 m elevation. A. albopictus have been reported to be minor vectors of avian malaria (Boyd 1949), and our attempts to transmit P. r. capistranoae with this vector were unsuccessful. It may be responsible for some malaria transmission in wild birds, but we feel that its role in Hawaii is minimal.

Experimental Results

Altitudinal Exposure Experiment -- None of the Laysan Finch which were exposed for a 12-day period at each of the 16 study sites contracted malaria. It may have been that the cages were placed too high in the trees, but this is the vertical height strata where many native birds feed (pers. observ.). Perhaps, because of decreased vector densities, a longer exposure period is necessary than when Warner (1968) conducted his work. However, during the course of the study rodents chewed holes in the mosquito screen on the large holding aviary at the Avian Disease laboratory (1200 m elev.) which housed Laysan Finch and Palila (Psittirostra bailleui). The date at which the holes were chewed was not precisely known, but the birds may have been exposed for at least a four-week period. Four of the Laysan Finch and two Palila contracted malaria; medication was given to the birds and one Palila survived.

Asexual Malaria Cycle -- Our initial study strain of P. r. capistranoae (H-1) was established on 7 December 1977 from a moribund Apapane. Several other strains originating from a wild-caught Japanese

White-eye, a House Sparrow and other Apapane were maintained in our laboratory, but when innoculated into canaries, no differences were observed in the morphology or pathogenicity of these strains.

Each avian host used in our experiments was put through a rigid acclimatization period after capture from the wild. These periods were quite variable between the eight challenged host species. Weight stabilization was achieved in the Canary, Red-billed Leiothrix, Japanese White-eye, Laysan Finch, and Amakihi within one week after capture. In fact, the Laysan Finch spent three weeks in small holding cages on their ocean voyage from Laysan Island, and arrived at heavier weights than when taken into captivity. The Iiwi adjusted more slowly, and weight stabilization was not achieved until an average of 76.6 (SE = 5.27) days following capture. Apapane, the most common honeycreeper, also had a difficult time in adjusting to captivity; an average of 71.4 (SE = 2.97) days elapsed before this species was ready for challenge experiments with the malaria parasite.

The five experimental Japanese White-eye and Red-billed Leiothrix were refractory to the *P. r. capistranoae* parasite, as were two of the Mauna Loa Amakihi (Fig. 8). All other challenged birds contracted malaria, although inter- and intraspecific survival rates were variable. Because two of the Mauna Loa Amakihi were refractory, their Index of Adaption (I_a = 0.60) was the highest of the native species. The next highest group was the Canary (I_a = 0.50), followed in decreasing order by the Mauna Kea Amakihi (I_a = 0.33), Apapane (I_a = 0.30), and the Iiwi (I_a = 0.20). The Laysan Finch totally lacked any immunogenetic capacity against the introduced *P. r. capistranoae* parasite (I_a = 0).

Although survival capabilities differed among the challenged native host species, parasitemia levels throughout the patent period were similar (Fig. 9). Peak parasitemia levels for the Amakihi, Apapane and Iiwi all fell within 400 parasites/10,000 RBC of one another. In the one Laysan Finch which survived past day 20 of the patent period, parasitemia levels were dropping, although the bird did not survive. The disparity of parasitemia levels between the native Hawaiian species and the Canary indicates the very high susceptibility of the native birds to this introduced malaria parasite. Moreover, the length of the primary attack period was over three times longer in the Hawaiian species. The duration of the primary attack in the main island Hawaiian birds did not correspond to the number of individuals that survived. Fewer Iiwi than Amakihi or Apapane survived the infection, but the latter species carried much higher parasite levels for a longer time period. However, analysis of the overall course of the infection does show that the prepatent period was shorter in the Iiwi, as was the initial period of rise. In addition, the length of the Iiwi crises was almost double that of the other two species.

In an analysis of immature (trophozoite), sexual (gametocyte), and asexual (schizont) forms present throughout the primary attack period in the Hawaiian bird hosts, trophozoites generally outnumbered the other two groups of parasites (Fig. 10). Parasite abundance patterns were similar in the Amakihi and Iiwi except that during the Iiwi crisis period schizonts outnumbered gametocytes. In the Apapane, the sexual and asexual forms comprised a much larger percentage of the total parasites than in any of the other species. The highly susceptible Laysan Finch, in addition to having an earlier expression of parasites in the peripheral blood, had a very different pattern of parasite abundances. Except during

a brief three-day period, schizonts outnumbered gametocytes. Moreover, a crisis period seems to have occurred in the mature sexual and asexual forms, but the immature parasites were still increasing at the time the last individual succumbed. Only in the Laysan Finch did we observe a decreased food intake just prior to death, and this was the only species which exhibited an appreciable weight decline over the patent period.

The daily schizogonic cycle in the blood was asynchronous when the parasites were analyzed as percentages of those counted on a single occasion as recommended by Garnham (1966). However, when expressed as the number of parasites per 10,000 RBC over a 24 hr cycle, periodicity of P. r. capistranoae in the Apapane, Amakihi and Canary exhibited a quartan cycle, with peaks occurring at approximately 12-hour intervals (Fig. 11). Peak levels of gametocytes in the peripheral blood occurred in the late morning and early afternoon hours.

Sexual Malaria Cycle -- The daily activity patterns of C. quinquefasciatus and A. albopictus were antipodal (Fig. 12). C. quinquefasciatus were more active during the cooler night (viz. 1800-0600 hrs), whereas A. albopictus exhibited the greatest activity during the warmer daylight hours. The only time of the day when the activity of the two species overlapped was from 1800-2200 hrs. Forty-six separate feedings, employing 172 C. quinquefasciatus, were conducted during the course of this study. A total of 24 A. albopictus were engorged on infected birds in eight separate feedings, and none became infected. C. quinquefasciatus would not feed during the day (n = 12 replications), and it was necessary to leave infected birds in the biting cages over night.

The sexual stage of the malaria cycle was quite difficult to complete, probably because of the low ambient temperatures at the laboratory (which

was at 1200 m elevation). Colder temperatures are well known to inhibit parasite development in the mosquito (Hewitt 1940, Ball and Chao 1964, Huff 1968). The earliest ookinete development was observed 16 hours after engorgement, and the parasite reached this state of development in numerous C. quinquefasciatus. Early ookinete measurements ($\bar{X}$ length = 6.5μ, SE = 0.61; $\bar{X}$ width = 2.2μ, SE = 0.22) were similar to those given for other strains of P. relictum (Corradetti et al. 1970). However, we found a very low incidence of oocyst development in the gut wall. It was not until second blood meals were started that infection rates in the mosquito reached high enough levels to consistently complete the sexual cycle. Sporozoite development was quite slow, and it was not until day 16 that completion of the sexual cycle in the mosquito was achieved (Table 4).

Successful transmission of P. r. capistranoae by C. quinquefasciatus was first demonstrated in this study on 28 September 1979. The mosquito took its initial blood meal on 12 September from an Amakihi with a parasitemia level of 1500 parasites/10,000 RBC. Sixteen days later the mosquito engorged a second time on a noninfected Laysan Finch. Through day 4 the Laysan Finch exhibited no signs of parasitemia in the peripheral blood. The first parasites were observed on day 5, the infection climax was reached on day 7, but the bird did not die until day 21. When compared to the cycle of subinnoculated Laysan Finch (see Fig. 9), these data indicate that the malaria cycle in sporozoite infected individuals takes longer to develop than in subinnoculated hosts.

DISCUSSION

In this section of the paper we will concern ourselves with answering four basic questions: (1) What is the present day distribution of the malaria parasite on the island of Hawaii? (2) How susceptible to malaria are the native land birds, when compared to their introduced counterparts? (3) What selective forces are currently operative on the bird populations, and how are the birds coping? (4) What role has malaria played in the decline of the endemic Hawaiian avifauna?

Malaria Distribution

Although Warner (1968) presented few data on the altitudinal distribution of malaria and mosquitoes in Hawaii, he suggested that the vector, C. quinquefasciatus, was "functionally" absent from the forests above 600 m elevation; therefore, this habitat was a "safe" or malaria free zone. Our data indicate a quite different picture. Breeding populations of the vector are present in the forests on Mauna Loa throughout much of the extant native bird habitat, and infected birds are found at all elevations on the mountain. During the warmer months of the year C. quinquefasciatus can be found breeding even in the uppermost reaches of the mesic forest. However, during our 3-year study we rarely observed free-flying adult C. quinquefasciatus, and the negative results of our biting experiments show only too well how difficult it is to determine the presence of this vector. The daily activity cycle of C. quinquefasciatus is asynchronous with that of man's, and thus the mosquitoes often avoid detection. Furthermore, Tempelis et al. (1970) showed a definite preference of this mosquito to bite birds, thus further reducing the chance of human detection. However, the 30% infection rate

of the Apapane population is evidence that avian malaria transmission in Hawaii does occur quite successfully at relatively low detectable vector densities.

There is the possibility that C. quinquefasciatus, in the absence of natural selective forces present in its native North American habitat, has recently undergone an altitudinal expansion, but the data presently available does not completely support this hypothesis. It would have meant that the mosquito was restricted to elevations below 600 m from 1827 until c. 1960, after which it suddenly evolved during a 15-year period the ability to more than triple its altitudinal range. The likelihood of this rapid expansion is further diminished by the fact that extensive mosquito control programs were initiated in Hawaii during the early 1960's. We feel this vector was present above 600 m when Warner conducted his initial malarial survey, but, as is the case today, in low enough densities so that it was not detected on a regular basis. Furthermore, as noted by Goff and van Riper (1980), the distribution of the mosquito is not uniform at higher elevations, but coincides with the distribution of kipukas. This disjunct distributional pattern, combined with primary breeding sites being other than ground pools, would make the detection of the mosquito at higher elevations unlikely. This is supported by the pattern we see today with casual observations of mosquitoes at higher elevations (Komatsu 1966, Banko in Berger 1991) which are similar to those earlier observations of Sweezy and Williams (1932).

The presence of a vector does not necessarily imply that malaria can be transmitted in that location. However, we found malaria present at all locations we sampled from sea level to the highest forests. Some of the birds at the higher elevations undoubtedly contracted the malaria during

their sojourns to the lower forests, particularly those infected individuals captured at the upper xeric stations. But the high levels of infection at 1350 m in the xeric and 1500 m elevation in the mesic forest can be attributed only to the fact that C. quinquefasciatus breeds at those locations throughout the year.

The present day altitudinal distribution of the malarial parasite on Mauna Loa is therefore not a direct reflection of vector densities (Fig. 13). C. quinquefasciatus are numerous at lower elevations, yet the malaria level in avian hosts from those localities is quite low. It is not until the mid-elevational ranges are reached that malaria levels in the avifauna appreciably change, and these are also the lowest elevations at which the native birds are presently found. In this region of overlap, malaria levels increase disproportionately to the number of available vectors. As noted by Goff and van Riper (1980), it is at these elevations that the kipuka begins to function as a mechanism for increased contact between vector and host, thus increasing the potential for small vector populations to efficiently transmit the malaria parasite to a large number of hosts. It thus appears that a directional selection pressure, exerted by the pathogenicity of the malaria parasite, is presently forcing the native avifauna into the highest forest areas.

The distributional pattern of malaria in Hawaii today is by no means a static situation. Temperature and rainfall patterns have a marked effect upon levels of malaria in the avian populations, particularly at the mid-and upper elevational forest areas. The warmer fall months allow C. quinquefasciatus to breed at higher densities in the upper forest reaches (Goff and van Riper 1980), and probably also enhances the survival and completion of the parasite's sexual cycle in the insect host.

Concomitantly, higher levels of malaria infections in the avian populations occur with the upper altitudinal movement of the vector. However, it is now certain that avian malaria and its vector are distributed from sea level to at least 1500 m throughout the year in the forests on Hawaii.

Susceptibility of Hawaiian Birds to Malaria

Field data and laboratory experiments have shown that in all cases the native birds are more susceptible to malaria than are introduced species (Fig. 14). This result is not surprising when one considers that malaria is relatively new to the Hawaiian Islands. In perceiving the total lack of resistance to malaria in the Laysan Finch, whose population has never been exposed to this parasite, one obtains an insight into the immunogenetic capabilities of the early Hawaiian avifauna. There apparently was very little. The explosion of malaria parasites following the prepatent period (see Fig. 9) predetermined that the early birds either survived or succumbed; a gradual adaptation was rarely possible. The absence of weight loss and the continued high levels of fat in our challenged birds attests to the fact that infections are still acute in nature. From those few early individuals that did survive, the immunogenetic capability to cope with the malaria parasite has now spread throughout portions of the extant populations.

We found that each challenged species had a differing resistance to the malaria parasite, and the degree of susceptibility appears to be a direct reflection of the present-day abundance of that species. For example, the Iiwi was the most susceptible of the challenged birds from the main islands, and has undergone the greatest population declines. In 1903 Perkins wrote: "The 'Iiwi' is one of the most abundant and generally

distributed of all of the Drepanid birds, being found throughout the woods of all the forest-clad islands." Now Iiwi are rare on Oahu (Shallenberger 1978) and Molokai (Scott et al. 1977), and apparently extinct on Lanai (Hirai 1978). Since Baldwin's 1953 work on the island of Hawaii, the species has also undergone drastic population reductions and range contractions (Conant 1981, Scott et al. in press). On the other hand, the Amakihi, which we found to be the most resistant native bird, is still found in fairly high numbers throughout the islands. In some cases, this species has reinvaded areas from which it was earlier extirpated (Berger 1981, Pedley 1961, van Riper 1973).

Each bird species appeared to cope with the high parasitemia levels in a different fashion. The Mauna Loa Amakihi was the only native bird which was refractory to the malaria parasite, and all but one of the challenged individuals survived. The relatively high degree of immunity developed by this bird can be linked directly to its lifestyle. Unlike the Apapane and Iiwi, the Amakihi is fairly sedentary and does not undergo regular massive population shifts (Baldwin 1953). This would mean that any population found within the "malaria zone" would be continually exposed throughout the year. Thus, the selective effect for immunogenetic capabilities would be greater than for species which migrate out of the zone during the breeding period.

The differences that have developed in regard to the immunogenetic capabilities of a species is exemplified by the comparison of the wet forest Mauna Loa and dry forest Mauna Kea Amakihi populations. Malaria is absent in the dry forest of Mauna Kea (van Riper 1975), and the Amakihi from this region, unlike the Mauna Loa Amakihi population, were extremely susceptible to malaria (Fig. 8). This indicates that intraisland gene

flow is quite slow in Hawaii, as recently suggested by Pratt (1980) for the Hawaii Elepaio (Chasiempis sandwichensis). However, the immunogenetic ability to resist P. relictum is now definitely present in a number of the main Island endemic Hawaiian birds, and should stand them well barring the future introduction of another malaria species.

As mentioned previously, the Iiwi was the least resistant of all the main Island endemic passerines that we challenged. The malaria crisis period was longer than in any other host and more individuals died. It is puzzling why this species should lag so far behind others in its ability to cope with the malaria parasite. Perhaps because of the bird's past frequent migrations to lowland areas (Perkins 1903), an earlier epizootic such as avian pox reduced the population to such a level that gene flow for immunogenetic resistance to the newly introduced malaria parasite was impaired. This hypothetical initial population reduction would have been compounded by the extreme bill specialization of the bird and its inability to cope with the altered habitat and interspecific competition (Pimm and Pimm in press). However, the fact remains that this difference in immunogenetic capabilities may be only a reflection of the species genetic inability to cope with the malaria parasite.

The Apapane was of intermediate resistance to the P. r. capistranoae parasite, but unlike the other hosts had a prolonged patent period (Fig. 9). This was undoubtedly the reason why the Apapane had the highest population infection levels that we recorded during this study. We propose that the Apapane is now in an intermediate evolutionary period in which the bird is adapting to the malaria parasite.

The above observations would suggest the following pattern for an evolutionary sequence of resistance to the malaria parasite: (1) Totally

nonresistant birds would have an early (relative to the rest of the group of host species) expression of parasites; the crisis period would occur at higher parasitemia levels and the great majority of individuals would succumb to the infection, as exemplified by the Laysan Finch. (2) In the next phase, as occurred in the Iiwi, first expression of peripheral blood parasites would appear later; parasitemia levels would be relatively lower during the crisis period but the duration of the crisis would be extended; most infected individuals would die, but in those that survived the patent period would quickly abate. (3) The next phase follows the pattern of the Apapane in which the time of first parasite expression appears to be fixed for the host species, as does the peak of parasitemia for that particular malaria parasite; the crisis period shortens, more individuals survive the initial explosion of parasites, and the patent period is greatly extended. (4) The next sequence of evolutionary immunogenetic events involves a shortening of the patent period with all other parameters of the infection remaining the same (e.g., the Mauna Loa Amakihi population). (5) The final stages of evolutionary resistance might take either of two directions depending upon the host response to the parasite; the host would either develop a refractory ability as in the Japanese White-eye, Red-billed Leiothrix, and some of the Mauna Loa Amakihi, or, as in the Canary, suppression of parasite numbers in the host would occur so that the crisis level was not as high, and the patent period was shortened and not as severe.

Forces Presently Operative on Native Bird Populations

The results of this study leave little doubt concerning the adverse impact that avian malaria is having on the native landbirds of Hawaii. It is evident that strong selective forces are in operation which limit

native birds to select habitats on Hawaii. For example, as well as restricting these birds to the higher elevations, there is a directional pressure forcing birds to the drier areas. The malaria parasite also generally depresses native bird population numbers. In addition, host behavioral patterns have been modified so that the birds now minimize their temporal contact with the malaria vector.

Immunogenetic Mechanisms -- The mesic forests of Mauna Loa occupy a much larger area and have a higher insect biomass and standing crop of nectar producing flora than does the xeric forest (Mueller Dombois et al. 1981). One would therefore expect a greater density of birds in the mesic habitat. In comparing capture rates of birds banded during the same time period at mesic and xeric stations of similar elevations, our mist-net data indicates that this was not the case. For example the Apapane, which is principally a "wet forest" bird (Berger 1981), was captured more often at xeric sites than at mesic sites of similar elevations (5:4 ratio). The Iiwi, another "wet forest" bird, also had higher capture rates at xeric sites. The higher capture rates in xeric forest may be a result of the "catchability" of the birds in that habitat, but nevertheless does indicate that "wet forest" birds are presently found in quite high densities throughout the year in the drier areas. The results of a recent census of the birds on Hawaii also shows that highest native species densities occurred in the high xeric forests (Scott et al., in press). Because of the availability of vector breeding sites, avian malaria levels were uniformly higher in the mesic areas. It therefore appears that as well as restricting the birds altitudinally, pressure from the malaria parasite is forcing native birds into the drier areas.

On the other hand introduced birds, except for the House Finch which is primarily a dry-forest species, were consistently found in higher numbers in the mesic forests. For example, the Japanese White-eye which is ubiquitous throughout the islands (Guest 1973), was captured at higher levels more often in mesic sites (9:1 ratio). It therefore appears that the introduced bird species are preferentially selecting those areas where native species occur disproportionately in lower numbers, and the refractory ability of many introduced species to the malaria parasite certainly benefits them in these areas.

With the primary native bird breeding period from January to May, highest population levels would be expected in June, after first year birds have been added to the population. This was not the case; there was instead a decrease in the total number of birds captured/100 net hours during this period (see Fig. 2). This decrease can be attributed directly to the impact of malaria, because there is at this time a sharp increase in the number of infected birds. We found significantly higher parasitemia levels in younger birds although they were not differentially being infected), and it is probably the death of many individuals in this age group, in concert with the attrition of some adult birds, which contributes to the low population levels during the postbreeding period of the annual cycle.

Nonimmunogenetic Mechanisms -- Certain nonimmunogenetic pressures are also exerting themselves which modify the behavior of native birds. Warner (1968) noted that in his experimental Hawaiian birds, none slept with their bill and face into the fluffed black feathers, and that their legs were continually exposed. We have made extensive observations on the sleeping postures of the captive birds from Kauai and Hawaii. Kauai

Amakihi and Apapane frequently maintained a sleeping posture with the bill and face tucked into the back feathers and often had one leg raised into the abdominal feathers. In the birds maintained on Hawaii Island during this study, the Amakihi, Iiwi, and Apapane all slept in this above mentioned fashion. On a few occasions, individuals were found in a sleeping posture in which they were clinging to the sides of the cages. But for the most part, all drepanidids that we have observed slept with their heads tucked into the ruffled back feathers and one leg raised and tucked into the breast feathers.

During the warmer months of the year, a number of native birds rely upon nectar as a food source, and follow the altitudinal flowering sequence of nectar-bearing trees (Baldwin 1953, Munro 1944, Perkins 1903). Lamoureux (1973) has shown that the Hawaiian nectar-producing trees bloom along an elevational gradient, with greatest flowering at lower elevations during the summer and fall period, gradually progressing upslope with the highest altitude trees flowering during the winter months. This means that in order to obtain maximum quantities of nectar, birds must move to lower elevations during the fall period. It is during this time that the greatest number of birds are found with malaria. The birds are therefore forced into the lower malaria belts during their fall sojourns in search of nectar, and are met at this time by an expanding vector population. As a result, the zone of mosquito-bird overlap is greatly increased and the potential for malaria tramsmission is much higher than it otherwise would be. It can be seen that interacting environmental and behavioral activities are directed toward maximization of the spread of avian malaria.

Another nonimmunogenetic adaption in reference to the above mentioned phenomenon of altitudinal flowering, has been the development of a behavior in which some native Hawaiian birds physically remove themselves each day from the malaria zone. MacMillen and Carpenter (1980) have shown that the Apapane and Iiwi presently undergo daily altitudinal migrations. Individuals gradually move downslope during the day, then just prior to dusk gather from the lower elevations (c. 1200 m) and migrate upslope converging on a common "roosting" area at approximately 1700 m elevation. Although these daily flights are energetically costly, these authors felt that the overall overnight energy savings, as a result of the thermal protection afforded by the mature forest, compensated for these movements. Apparently these flights occur only in the warmer, and usually drier months of the year. If in fact the selective force for this movement was energetically based, one would predict that these flights would occur during the colder and wetter winter months. We have found that these two species regularly breed during the cold-wet winter months at all elevations we sampled, and our mist-net recapture data and color-band observations show that most birds are also sedentary during this breeding period.

We suggest that the daily evening movement to a higher elevation is a direct consequence of the selection pressure exerted by the malaria parasite at lower elevations. The common overnight location identified by MacMillen and Carpenter (1980) is directly adjacent to our 1650 m mesic study site, and at this location we found our lowest level of malaria infection (see Fig. 5). The birds leave the overnight area early in the morning, when C. quinquefasciatus activity levels are decreasing (see Fig. 12), gradually work downslope, and reach the lower elevations when C.

quinquefasciatus is at its lowest activity levels. MacMillen and Carpenter showed that the evening flights began at 1600 hrs and most birds reached the upper elevations by 1830 hrs. Our data indicate that C. quinquefasciatus activity does not begin until 2000 hrs, at which time the birds are absent from the principal malaria belt.

What was once probably a gradual movement of the birds downslope following the flowering of nectar-producing trees has now evolved into a daily circular pattern (Fig. 15). In the past, those birds that either remained in the breeding area or that moved laterally across the mountain (Baldwin 1953, van Riper 1978) would not have been appreciably affected, nor would have the small segment of the early Apapane and Iiwi populations which returned upslope each evening. However, those individuals which gradually moved downslope would have eventually had to overnight in an area of high malaria concentration. Owing to the extreme susceptibility of the early drepanidids (using the Laysan Finch as an index), the great majority of those individuals most likely succumbed to malaria. At present, that portion of the population which still undergoes the gradual downslope movement is being further reduced in numbers. Because of the selective pressure exerted by the malaria parasite at lower elevations, we are therefore left today with a pattern in which the large majority of the Apapane and Iiwi undergo daily altitudinal migrations.

Malaria Arrival Date

Given the impact that P. r. capistranoae is presently having upon the native Hawaiian birds, the question arises as to the date this parasite was introduced into the islands. It is generally conceded that avian malaria may have been present in the vector-free Hawaii before historic times because of the arrival from time to time of parasitized migrants,

and that after the introduction of C. quinquefasciatus in 1826 the parasite rapidly spread over the island chain (Warner 1968). There remains some doubt to us that a large enough reservoir of malaria was present at this early date, and that it was from this source that malaria spread to the native birds and resulted in the innumerable extinctions in the late 1800s.

If in fact malaria was a causative factor in the demise of the native birds at the turn of the century, one surely would have expected it to be common on Hawaii Island during the late 1930s. This was not the case. Baldwin (1941b) did a survey of blood parasites throughout Hawaii Volcanoes National Park in 1938-39, collecting samples from 88 introduced and native birds. He collected birds from 700 m to 2000 m elevation, and the only species in which he detected malaria were the introduced Red-billed Leiothrix (collected at 1350 m elevation) and the California Quail (collected at 2000 m elevation). Baldwin concluded his study by saying: "This is at least some indication that there was no high incidence of bird malaria in the native birds and possibly none at all." In the same areas where we found extremely high levels of malaria in the native birds, he failed to find any. It would have been virtually impossible for him to overlook this parasite if it had been present.

The largest number of migrants to Hawaii are sea- and shorebirds, which regularly travel from North America and Asia. Recent exhaustive studies concerning distribution of hematozoa in bird families across North America (Greiner et al. 1975) and Asia (McClure et al. 1978) have shown that both groups of birds are nearly hematozoan-free. Moreover, not one of the individuals examined by these authors were found to harbor P. relictum, the only malaria parasite presently known to occur in Hawaii

(Laird and van Riper, in press). Ducks each year reach Hawaii on a regular basis, and are the only migrant host group known to carry P. relictum, although P. r. capistranoae has never been reported from them. The strenuous c. 4,500 km trip from the mainland would most certainly select against the arrival of any individual with a high malaria parasitemia. Moreover, there is relatively little habitat suitable for migrating waterfowl in Hawaii, and these areas are restricted to select locations along the shorelines. Even during the late 1800s the native passerines rarely frequented these shoreline areas unless blown from the higher forests by storms (Henshaw 1902). It therefore seems unlikely that migratory birds could have acted as a substantial reservoir of avian malaria in Hawaii.

The Red Jungle Fowl (Gallus gallus) was probably the first avian introduction to Hawaii, and it is presently believed that the Polynesians brought this bird with them when they settled the archepelago (Berger 1981). Although little is known about the former range of this bird in Hawaii, Schwartz and Schwartz (1949) reported that it included parts of the forest from 2130 m elevation to sea level on all major islands. It is doubtful, however, that this species could have acted as a reservoir for the malaria parasite because Garnham (1966) found that chickens were scarcely, if at all, susceptible to infections of P. relictum. Moreover, if chickens were harboring P. r. capsitranoae, agricultural research investigation would assuredly have noted its presence in Hawaii long before now.

The complete asynchrony of P. r. capistranoae gametocyte periodicity and C. quinquefasciatus activity levels also suggests that malaria has been a recent arrival to the Hawaiian Islands. Gametocyte production

peaks during 1200-1500 hrs (see Fig. 11), whereas the vector activity levels peak during 2400-0300 hrs (see Fig. 12). This means that when C. quinquefasciatus is actively seeking blood meals the sexual malaria parasites are at their lowest levels in the avian hosts, thus decreasing the possibility of successful completion of the malaria sexual cycle. There apparently has been insufficient time for sexual parasite production to synchronize with vector prevalence levels.

In light of the above facts, we propose that the vector, C. quinquefas- ciatus, arrived well before an adequate reservoir of the malaria parasite was present. It seems likely that avian malaria was not permanently established in Hawaii until after the numerous releases of introduced birds following 1900. Although early release records are extremely fragmentary, Caum (1933) listed 93 exotic birds that had been released, Bryan (1958) included 95 species of introduced or escaped cage birds in his check list, and Walker (1967) noted 78 kinds of potential game birds released in Hawaii. The majority of species that successfully established populations in the native forests after release were liberated following the 1900s (Berger 1981). It is also interesting to note that the type host of P. r. capistranoae, the Painted Quail (Coturnix chinensis), was first introduced into Hawaii from the Orient in 1910 (Laird and van Riper, in press). Certainly after 1920 a large enough pool of introduced avian hosts was present in Hawaii to begin the spread of malaria to the native bird species.

The pattern of historic native Hawaiian bird decline is bimodal, and supports the above hypothesis concerning the late introduction of malaria to the archepelago (Table 5). The initial reduction of native birds occurred in the mid- and late-1800s, and was unlikely to be the result of

the malaria parasite, because many of the species that were extirpated during this period (e.g., the finch-billed drepanidids from Kona) were historically confined to elevations well above 600 m. The second extinction period started in the early 1900s and was most likely the result of the newly introduced P. r. capistranoae parasite. The birds that succumbed during this period were principally species that were found in the mid-elevational forest areas, that region where we found the highest incidences of avian malaria.

In concert with the second phase of extinction was a continued range reduction in many of the extant bird populations. This too can be fixed directly to the later introduction of malaria. Munro (1944) spent many years on Lanai and documented the status of the native avifauna on that island. In 1923 he wrote that, if anything, he saw the native birds increasing, but by 1932 they were again declining in numbers. The pattern of the Ou (Psittirostra psittacea) decline throughout Hawaii is characteristic of those species which were greatly impacted by avian malaria. For example, Bryan (1908) found the bird quite abundant on Molokai, being encountered at every location he visited, but Richardson (1949) failed to find the Ou in 1948, and it has not been observed on the island since (Pratt 1973, Scott et al. 1977). Carlsmith (pers. comm.) observed the Ou in the Puna district of Hawaii island (elevation 900 m) with regularity in the 1930s, but by 1940 the species was no longer present in those forests. Baldwin found Ou commonly in Hawaii Volcano National Park in 1936 and 1938-40 (Richards and Baldwin 1953), but it became much less common thereafter (van Riper 1978, Conant 1981).

Baldwin (1941a, 1953), the first ornithologist to conduct systematic censuses of the Hawaiian avifauna, found Creeper, Akepa (Loxops coccinea),

Iiwi, Apapane, Amakihi, and Elepaio from 600 m elevation along the Hilina Pali Road in Hawaii Volcanoes National Park. Conant (1975) recently censused Baldwin's original study plots and found that in the lower reaches (600 m - 900 m) the creeper, Akepa, and Iiwi had disappeared. Our mist-net data support these findings. Furthermore, the native bird species that presently remain between 600 and 900 m elevation have undergone sizeable reductions in their population numbers. This pattern of bimodal native bird extinction and decline appears to be consistent with the hypothesis of a later malaria arrival date.

CONCLUSION

There remains little doubt that malaria has had, and is presently having a significant negative impact upon the native Hawaiian avifauna. The extinction of many species during the second and third decades of the 1900s, and subsequent range reductions of other species can be attributed directly to the presumed introduction date of the P. r. capistranoae parasite. However, we must look elsewhere to explain the reduction of the Hawaiian avifauna prior to 1910. We are only now just starting to comprehend the impact Polynesians had upon the native birds prior to the discovery of the Islands (James and Olson, in prep.). The introduction of Rattus rattus and R. norwegicus following the arrival of Europeans no doubt was also a major factor which contributed to this early decline of the native avifauna (Atkinson 1977). Major habitat modifications by man and by introduced ungulates certainly played a part in reducing bird population levels, as have the introduced pig, mongoose, and feral cat. If disease did play a role in the initial decline of the birds, a logical explanation would be an arbovirus such as Avian pox. Early collecters noted lesions on the native birds characteristic of those caused by the Avian Pox virus (Munro 1944, Perkins 1903, Rothschild 1893-1900, Wilson and Evans 1890-1899), and with the annual altitudinal migrations of many birds, this particular pathogen would have been rapidly spread throughout the forests. We are therefore left with a multiplicative picture for the demise of the native Hawaiian avifauna. Avian malaria has been only one of the many reasons for the decline of this unique group of birds, but is one of the major population regulating mechanisms operative in the Hawaiian Islands today.

GENERAL SUMMARY OF RESULTS

1. Over 4,000 birds were captured and marked during this study, of which 2,365 were analyzed for blood parasites. A total of 7.8% of all individuals was infected with malaria.

2. We found that at the present time there is apparently only one species of avian malaria in Hawaii, Plasmodium relictum ssp. capistranoae Russell 1932.

3. Other blood parasites such as microfilaria, babesoids, and trypanosomes were not detected during this study and appear to be absent in the birds on Hawaii.

4. Atoxoplasma sp. was identified in blood smears of the House Sparrow, Spotted Munia (Ricebird), Japanese White-eye (mejiro); this is the first record of this blood parasite in Hawaii.

5. The 'apapane population had the highest percentage of infected individuals, (29%), of all the bird species we examined.

6. The 'amakihi was the most resistant of the main island native birds challenged with malaria; the 'i'iwi was the least resistant.

7. Infection levels of introduced birds was low, averaging less than 5%.

8. Birds were more likely to be exposed to malaria in the months of July

through December; November and December were the months in which birds had the highest infection levels.

9. Young birds were not preferentially being infected with malaria, but once infected they had less chance of surviving than did adult birds.

10. Elevation had the greatest influence upon population infection levels of malaria in the birds on Mauna Loa, Hawaii. Highest malaria levels occurred in the mid elevation zones (1000-1500 m = below Hirano's store to Kipuka Ki) where native birds and mosquitoes overlapped to the greatest degree.

11. The daily movement pattern of native birds to higher elevations may be a direct result of the birds removing themselves each day from the malaria zone.

12. Native birds were seldom captured below 1000 m (3,000 ft.), most likely as a direct consequence of the impact of the malaria parasite.

13. Native birds were found at lower elevations in the dry (Hilina Pali area) as compared to the wet (Thurston lava tube to Mountain View) forests on Hawaii, presumably because of reduced malaria parasites in the dry forests.

14. Wet forest bird populations had higher levels of malaria than birds from the drier forests, presumably because of increased mosquitoes.

15. Introduced birds were captured in greater numbers where native birds were absent, suggesting that the introduced species are filling the voids created after native species have disappeared.

16. The night biting mosquito (Culex quinquefasciatus) was found to be the principal vector of bird malaria in Hawaii.

17. Primary mosquito breeding sites were tree holes, pig wallows, human refuse, and dead hapu'u trunks and stumps.

18. Mosquito distribution goes as high as upper Kipuka Ki (1500m elevation) in Hawaii Volcanoes National Park; breeding occurs at this elevation throughout the year. The mosquito distribution is not, however, uniform at higher elevations but coincides with the distribution of Kipukas.

19. It is believed that Plasmodium relictum ssp. capistranoae did not reach Hawaii until after 1900, probably through the numerous cage--bird releases that occurred during that period.

20. Avian malaria is one of the major bird population regulating mechanisms operative in the Hawaiian Islands today. Malaria is presently restricting the native Hawaiian land birds to the higher and drier forest areas.

MANAGEMENT RECOMMENDATIONS

I. PROBLEM

Results of this study show that the introduced avian malaria parasite is adversly affecting the avian resources of Hawaii Volcanoes National Park.

In 1978 the National Park Service issued "Management Policies" in which they state (p. IV - 12):

> "Manipulation of population numbers of exotic plant and animal species, up to and including total eradication, will be undertaken when ever such species threaten protection or interpretation of resources being preserved in the park."

There can be no question that the introduced malaria animal (parasite) is threatening the native bird community within Hawaii Volcanoes National Park, and management steps should be taken to reduce the population of this exotic animal.

It has been found in other situations that the ideal place in the malaria cycle to direct control measures is toward the larval stage of the mosquito. Mosquitoes need standing water to breed and without this water the mosquito can not reproduce and the malaria cycle is broken. Fortunately, because of the porous basaltic lava substrate of Hawaii's national parks, there is little standing water. What standing water that does exists in "natural" collection sites, usually dries up prior to the 10-14 days required for the mosquito larva to hatch. Moreover, the majority of sites in which we observed mosquito breeding were artifical and/or closely associated with human activity.

The following recommendations deal with ways by which National Park Service personnel can reduce the density of mosquitoes in the Park. These

efforts will ultimately help in reducing the impact that the introduced malaria parasite is having upon the native bird resources of the park.

Action Plan

In order to eliminate as much standing water as possible, we recommend that:

A. A master map of the park should be established and maintained at the Resources Management Office. On this map all identified standing water locations should be recorded and then crossed off after they have been eliminated.

B. All gutters on buildings within the park should be repaired and properly slanted so that water drains completely out of the system. The gutters should be periodically cleaned so that leaves do not plug the drains and create standing water which ultimately results in mosquito breeding habitat. The recommended schedule of cleaning is once during the winter months (November-March) and at least twice during the remainder of the year. A sample schedule for the gutter monitoring might be February, July, and September.

C. All construction sites should be properly drained so as to minimize areas with standing water. For example, the exercise track was not properly graded and standing water was often found in the center. At another location near the imu pit at the Research Center, metal roofing was left on the ground, water seeped between the sheets, and mosquitoes started breeding there. As well as monitoring present locations, all people concerned with future construction in the park should be made aware of this problem prior to working on that project.

D. Feral pig populations should be reduced, and where possible, eliminated within the boundaries of the National Park. A large portion of the recorded mosquito breeding sites were the direct result of feral pig disturbance. For example, pig wallows were major mosquito breeding sites as were fern (hapu'u) trunks that had been pushed over and the center eaten out.

E. When feasible, park personnel should carry machettes with them in the field so that they can cross-cut each of the prostrate hapu'u stumps they find which contain standing water. In addition, personnel should continue to remove all containers in the forests that might hold water, and thus act as a potential mosquito breeding site.

F. An effort should be made to reduce the number of water containers in the forests. Rain barrels should be emptied where feasible (e.g. Kipuka Ki fire cache, and at the end of the Hilina Pali Road). Old stock watering troughs should be removed, and active ones should be drained when not in use for an extended time period. Large water collections should be screened where feasible, and all future water collecting devices should have the prevention of mosquito entry in mind when being designed.

G. All park employees should be made aware of this problem by some educational device, perhaps initiated by interpretation. In this manner, when visitors and employees find bodies of standing water, the location will be reported and appropriate action can be taken by the Resources Management Staff.

II. PROBLEM

We have found two types of blood parasites in birds from Hawaii Volcanoes National Park: 1) malaria; and, 2) Atoxoplasma (Lankestrella sp.). The latter parasite has heretofore not been reported from Hawaii, and the pathogenecity of Atoxoplasma to native birds is not known. We have found heavy infections of Atoxoplasma in the introduced House Sparrow on Hawaii. Since the effects of Atoxoplasma on native birds is not yet known, a highly infected resident sparrow population could offer a significant reservoir of this disease.

House Sparrows are notorious for their affinity to man. In Hawaii Volcanoes National Park we have found them breeding primarily in and around human habitations. The buildings in the park which are utilized by Sparrows for nesting are relatively few, but being spread out and "molded" into the surrounding forest, sparrows frequently are found in the same areas as are many native bird species. Colonies of sparrows presently appear limited to the area near KMC (including the golf course), the residential area (including Volcano House), and the Hawaii Field Research Center area. Since these small sparrow colonies are quite far removed from source areas outside of the park, this introduced species can potentially be controlled.

Action Plan

In order to control sparrow populations in Hawaii Volcanoes National Park, we recommend that:

A. The park immediately obtain from Hawaii DLNR and the US Fish & Wildlife Service the proper permits for collecting House Sparrows in the park.

B. House Sparrows be removed from the park by the most humane and expediant means possible (we suggest that they can be discretely trapped by cages baited with bird seed).

C. All breeding areas be kept free of nests. For example, the automotive garage in the park was cleaned of nests twice during 1979, but the birds immediately returned. It is recommended that in areas such as the garage the eves of the building be permanently screened to prevent the entry of nesting House Sparrows. The continued destruction of nests and reduction of nesting sites might discourage other sparrows from establishing residency in the National Park.

D. Following erradication of the extant population, those few birds which have emigrated into the park should be disposed of on a biannual basis. A schedule for this monitoring scheme might be survalience and trapping once before the spring and once before the fall "malaria highs."

III. MANAGEMENT RECOMMENDATION SUMMARY

In order to follow-up this research we recommend that a monitoring program be initiated by the National Park in which:

(1) An effort be made to see if blood malaria levels are decreasing in the birds because of efforts put forth by National Park Service personnel toward reduction of breeding sites of the mosquito vector. It is recommended that personnel of the Resource Management Staff mist net birds in the vicinity of the Research Center for a period not to exceed one week, during the months of August or September, and November or December.

Each captured bird should be bled by a toe clip, a blood slide (smear) taken and the slide then immediately fixed in absolute methyl alcohol for 30 seconds. Following each capture period, the labeling on all slides should be checked and the slides then sent to the CPSU/UC at Davis for analysis.

(2) A rigid quarantine should be placed on all caged birds which are brought into the National Park. Just as all pet dogs are required to be on a leash, we recommend that all pet birds be restricted to inside cages. No captive bird should be allowed in an outside flight, unless the structure is mosquito proof.

It is felt that if the above management recommendations are followed, levels of avian malaria in the native birds in Hawaii Volcanoes National Park will ultimately be decreased.

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Table 1. Number of Birds Captured per 100 Net Hours From 1979-1980 on Mauna Loa, Hawaii.

Bird Species	Sample Size	Birds/100 Net Hours						Total
		Jan.-Feb.	Mar.-Apr.	May-June	July-Aug.	Sept.-Oct.	Nov.-Dec.	
Apapane+	308	32.6	23.1	60.1	40.5	32.9	14.2	203.3
Amakihi+	630	107.2	65.7	78.5	105.1	107.9	85.8	550.1
White-eye	1,177	85.6	175.3	188.5	70.6	155.9	120.8	796.7
Elepaio+	71	6.3	5.9	2.9	12.3	16.2	6.7	50.4
Omao+	55	3.1	13.1	5.2	2.7	3.7	7.7	35.4
Iiwi+	104	16.9	9.0	10.1	20.7	14.7	6.0	77.2
House Finch	78	3.2	12.5	17.3	11.5	12.2	2.1	58.9
House Sparrow	62	5.4	9.5	6.7	0.8	2.6	9.8	34.8
Cardinal	45	5.3	7.7	4.9	1.2	3.8	5.7	28.7
Leiothrix	37	0.4	4.3	7.5	5.0	3.5	1.7	22.4
Spotted Munia	120	3.8	15.0	11.1	12.0	15.7	18.3	75.2
Misc. Species*	15	1.3	1.1	5.4	1.4	0.3	7.2	11.3
Total	2,702	271.1	342.2	397.4	283.8	369.4	280.6	1,945.3

*Barred Dove (Geopelia striata), Spotted Dove (Streptopelia chinensis), Blue Pheasant (Phasianus versicolor), California Quail (Lophortyx californicus), Common Mynah (Acridotheres tristis), Hawaiian Creeper (Loxops maculata), and Akiapolaau (Hemignathus wilsoni).

+Denotes native Hawaiian species.

Table 2. Malaria Infection Rates Throughout the Annual Cycle in Birds from Mauna Loa, Hawaii

Months (sample size)	Percent of Population Infected		Total Percent of Individuals infected
	Mesic Forest	Xeric Forest	
January-February (243/177)	8.20	6.90	7.5
March-April (25/150)	10.20	4.00	7.9
May-June (109/77)	11.00	3.90	8.1
July-August (230/129)	6.10	4.70	6.0
September-October (396/180)	9.30	5.00	8.0
November-December (281/122)	11.0	6.60	9.8

Table 3. Malaria Infection Levels in Birds at Different Times of the Year from Mesic and Xeric Forests on Mauna Loa, Hawaii

Months (sample size)	Parasites/10,000 RBC		Total number of Malaria Parasites Per 10,000 RBC
	Mesic Forest	Xeric Forest	
January-February (243/177)	1.21	0.47	0.97
March-April (255/150)	0.95	0.04	0.60
May-June (109/77)	0.87	0.81	1.27
July-August (230/129)	2.48	1.60	3.26
September-October (396/180)	3.46	0.78	4.15
November-December (281/122)	1.51	1.82	2.11

Table 4. Success rate of sexual cycle transmission with P. r. capistranoae in Culex quinqefasciatus and Aedes albopictus in Hawaii.

Days Between Infective Blood Meal and Second Feeding	Number of Trials (N = 196 Mosquitoes)	Success of Sexual Cycle Completion	
		Culex quinquefasciatus	Aedes albopictus
6	4	-	-
7	2	-	
8	8	-	-
9	12	-	-
10	8	-	-
11	1	-	
12	1	-	
14	8	-	-
16	6	+	-
17	4	+	

Table 5. Presumed Extinction Dates of Native Land Birds from the Main Hawaiian Islands (Berger **1981**).

Species	Premalaria Extinction Period	Postmalaria Extinction Period
Rallidae		
Hawaiian Rail (*Pennula sandwichensis*)	c. 1885	
Turdidae		
Oahu Thrush (*Phaeornis obscurus oahensis*)	c. 1825	
Lanai Thrush (*P. o. lanaiensis*)		c. 1931
Meliphagidae		
Oahu Oo (*Moho apicalis*)	c. 1840	
Molokai Oo (*M. bishopi*)	c. 1905	
Hawaii Oo (*M. nobilis*)		c. 1935
Kioea (*Chaetoptila angustipluma*)	c. 1860	
Drepanididae		
Greater Amakihi (*Loxops sagittirostris*)	c. 1900	
Lanai Creeper (*L. maculata newtoni*)		c. 1935
Oahu Akepa (*L. coccinea rufa*)	c. 1900	
Oahu Akialoa (*Hemignathus obscurus ellisianus*)		c. 1935
Lanai Akialoa (*H. o. lanaiensis*)	c. 1900	
Hawaii Akialoa (*H. o. obscurus*)		c. 1935
Oahu Nukupuu (*H. lucidus affinis*)	c. 1875	

Table 5 (continued)

Species	Premalaria Extinction Period	Postmalaria Extinction Period
(Drepanididae)		
Oahu Ou (*Psittirostra psittacea*)	c. 1900	
Lanai Ou		c. 1930
Molokai Ou		c. 1920
Mauai Ou	c. 1900	
Greater Koa Finch (*P. palmeri*)	c. 1895	
Lesser Koa Finch (*P. flaviceps*)	c. 1895	
Grosbeak Finch (*P. kona*)	c. 1895	
Molokai Crested Honeycreeper (*Palmeria dolei*)		c. 1915
Ula-Ai-Hawane (*Ciridops anna*)	c. 1895	
Mamo (*Drepanis pacifica*)	c. 1895	
Black Mamo (*D. funerea*)		c. 1915

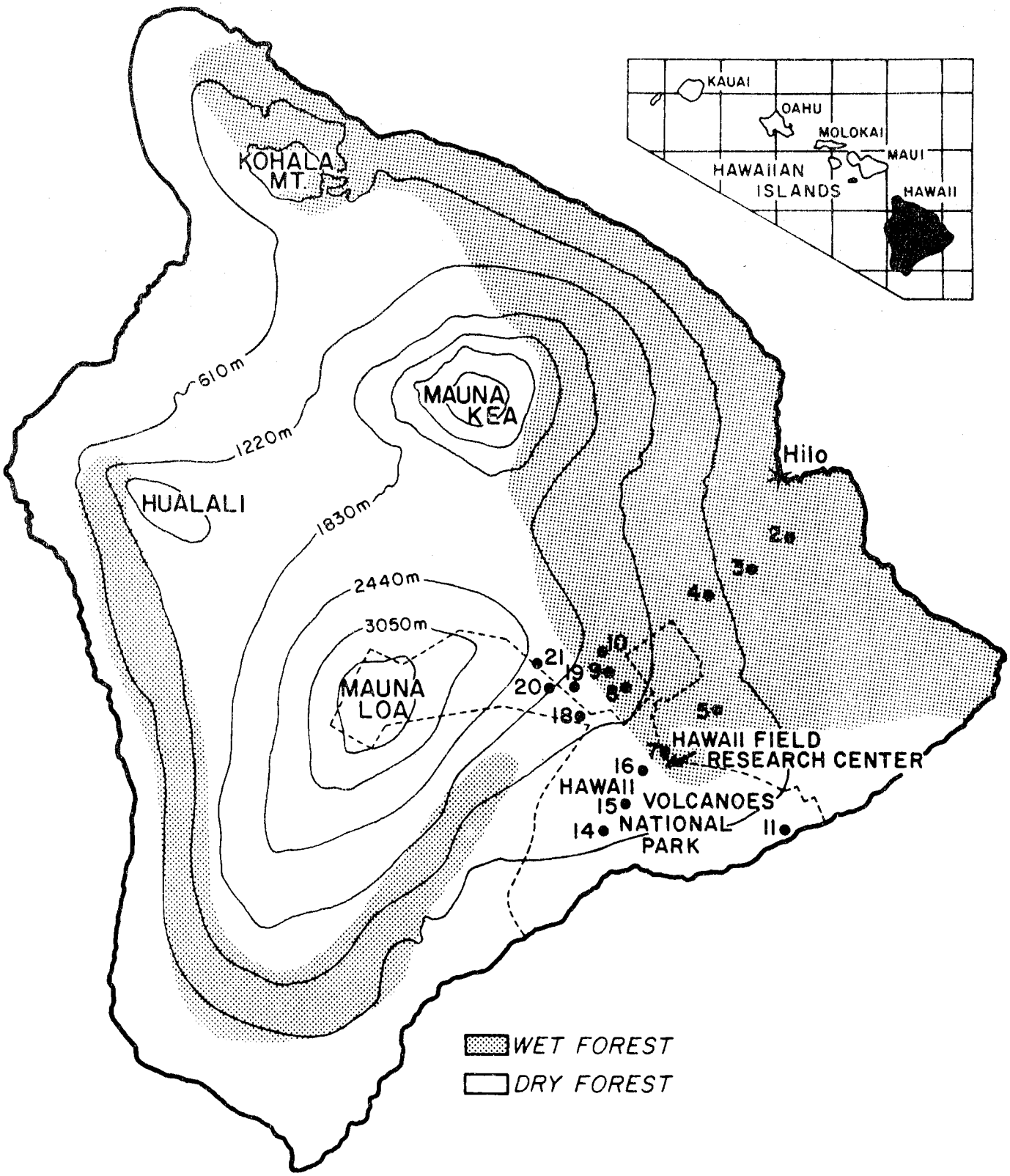


Figure 1. Location of study sites on the east flank of Mauna Loa Volcano, Hawaii.

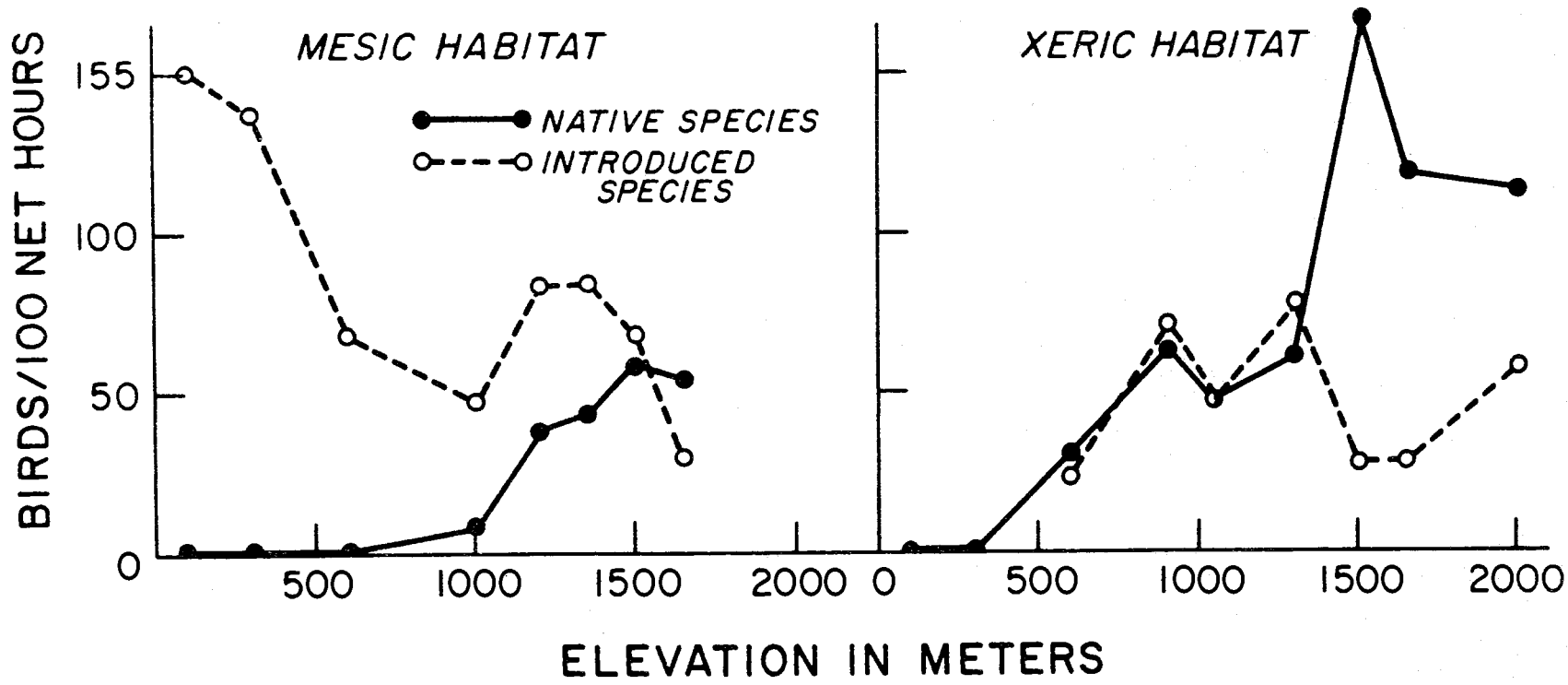


Figure 2. Total birds captured during the study.

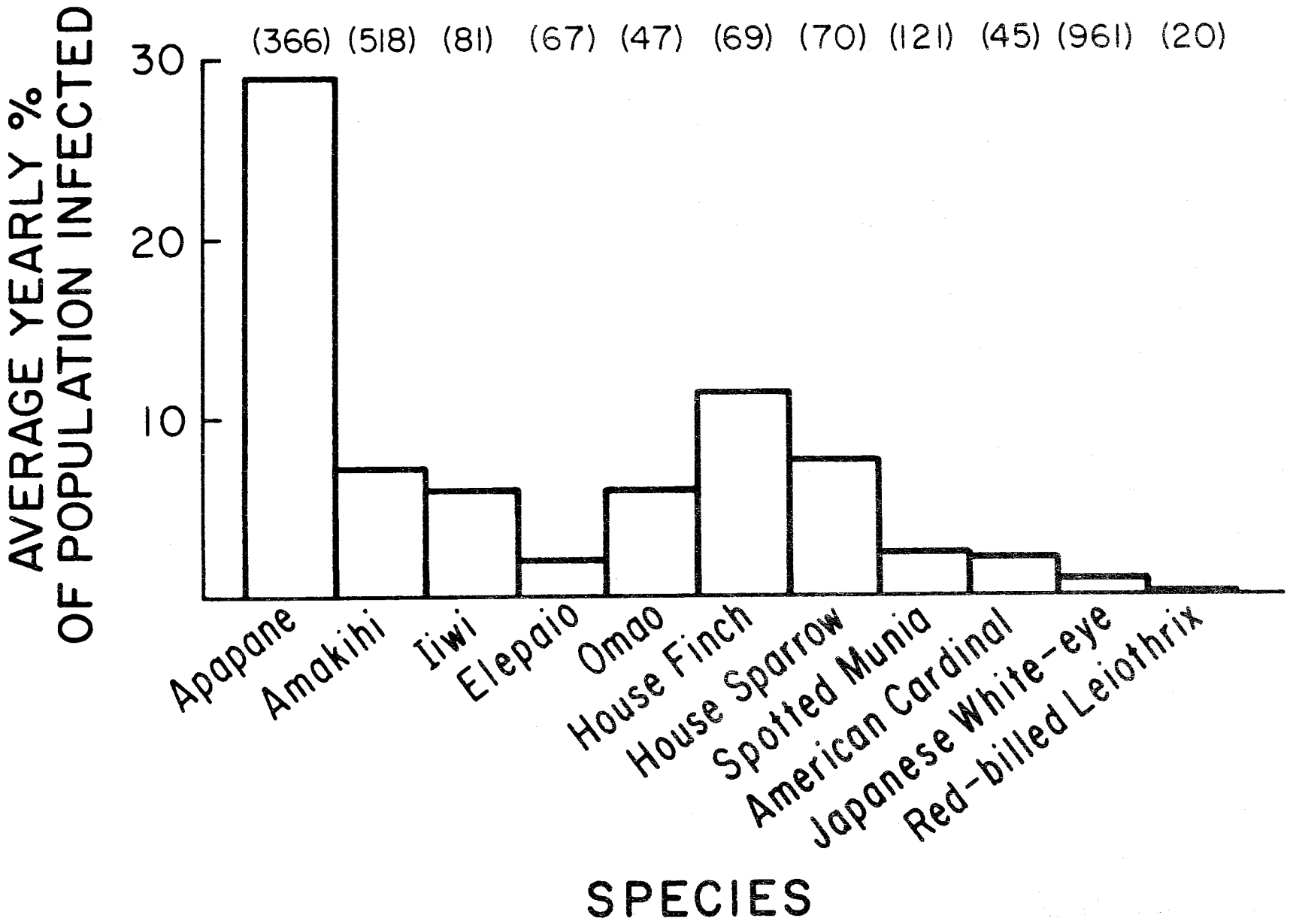


Figure 3. Average yearly percentage of birds infected with malaria on Mauna Loa, Hawaii.

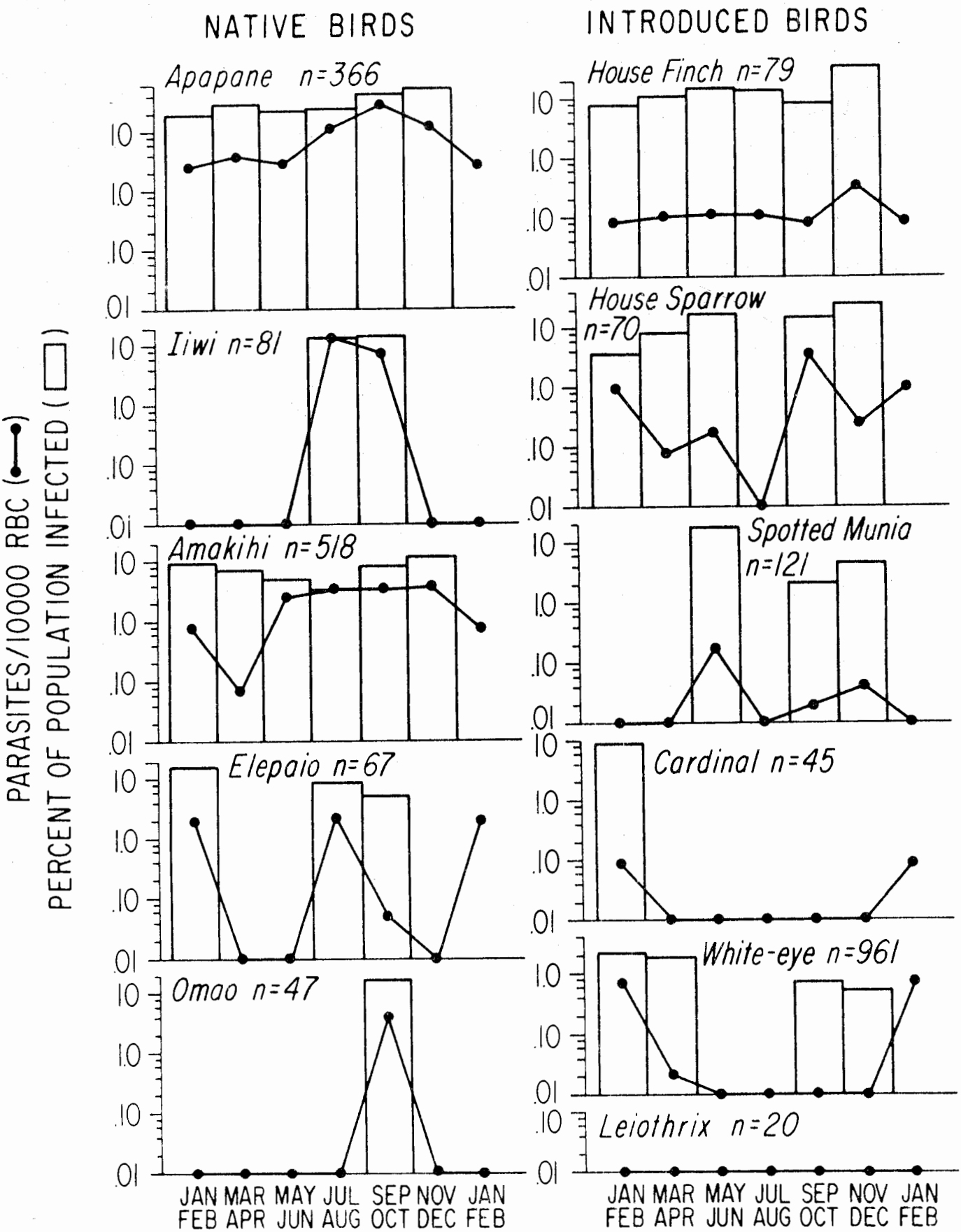


Figure 4. Yearly percentage of infected individuals infected and parasite levels of malaria in species of avian hosts from Mauna Loa, Hawaii.

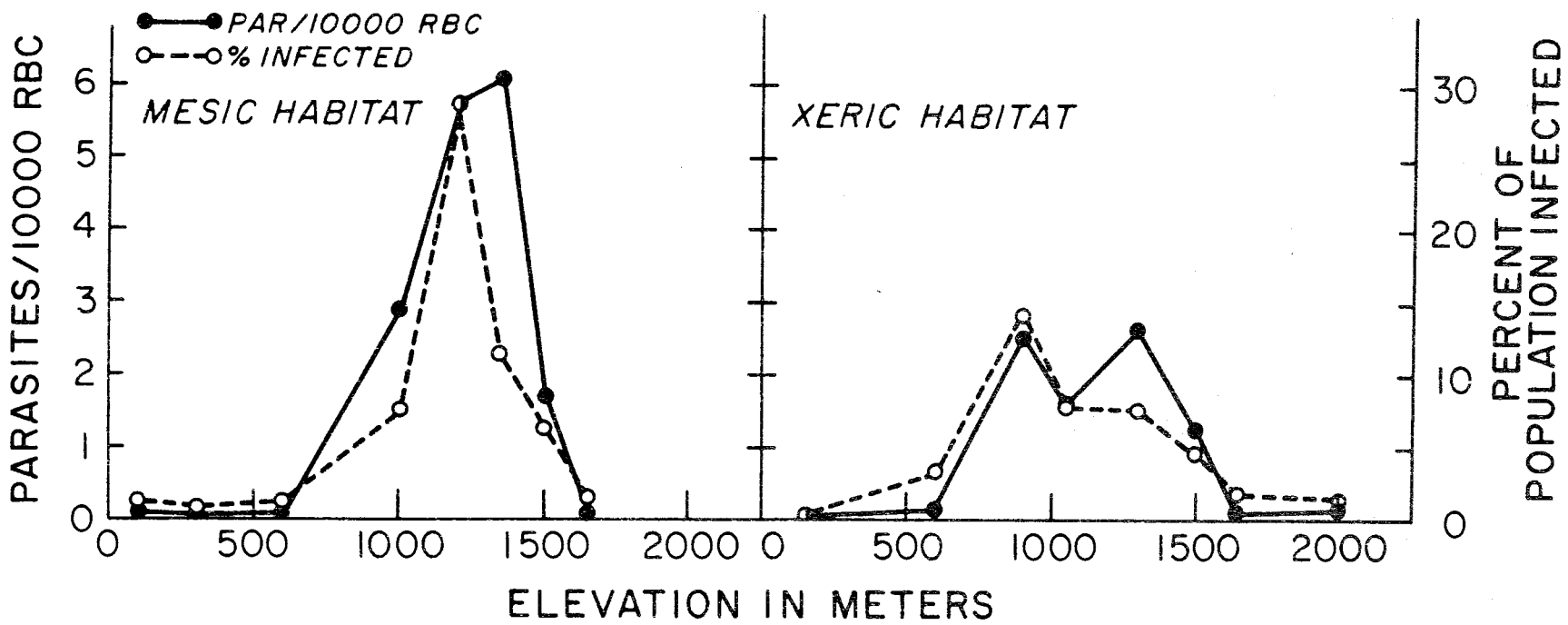


Figure 5. Infection rates and percentage of populations infected with avian malaria along an elevational gradient on Mauna Loa, Hawaii.

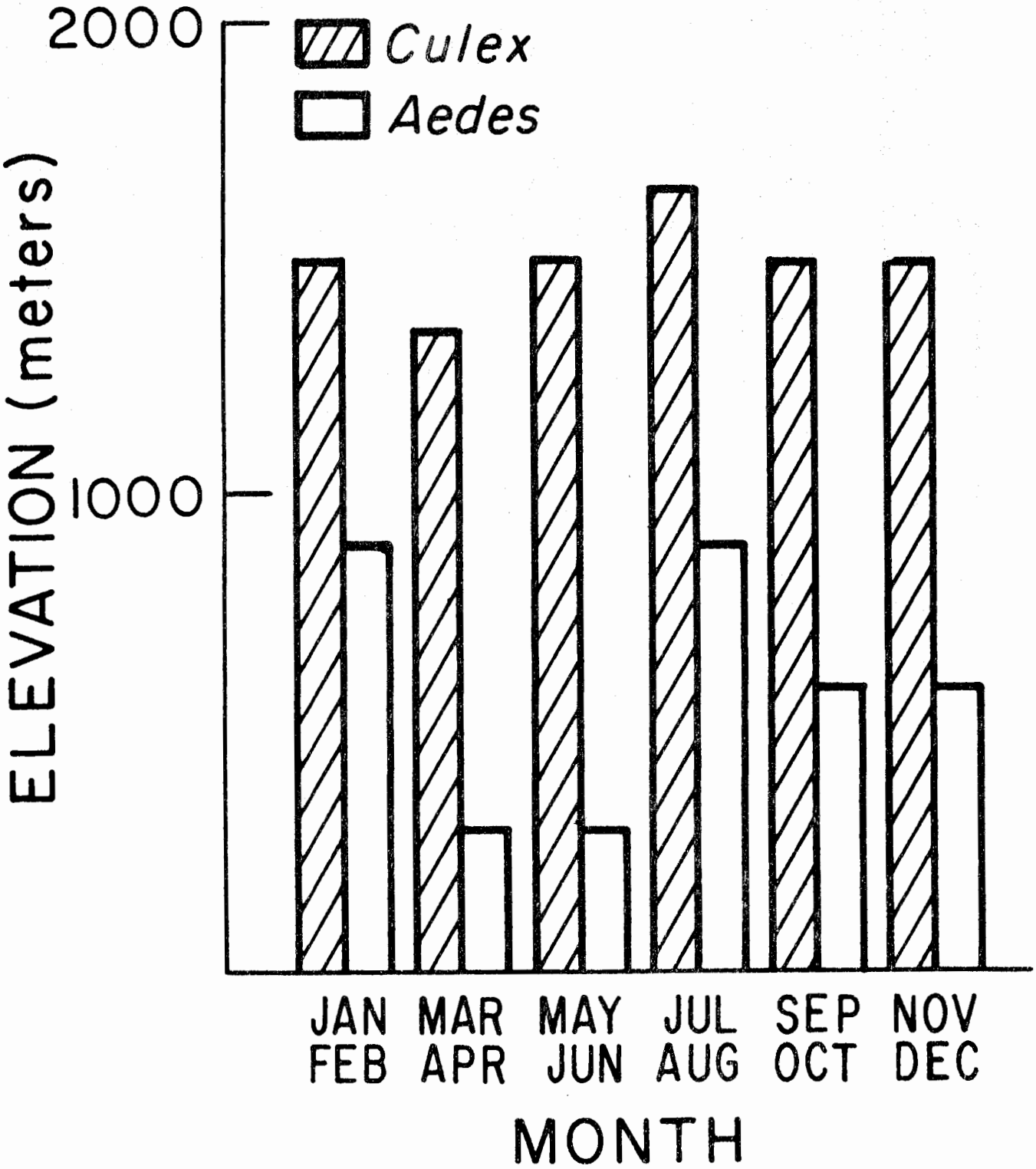
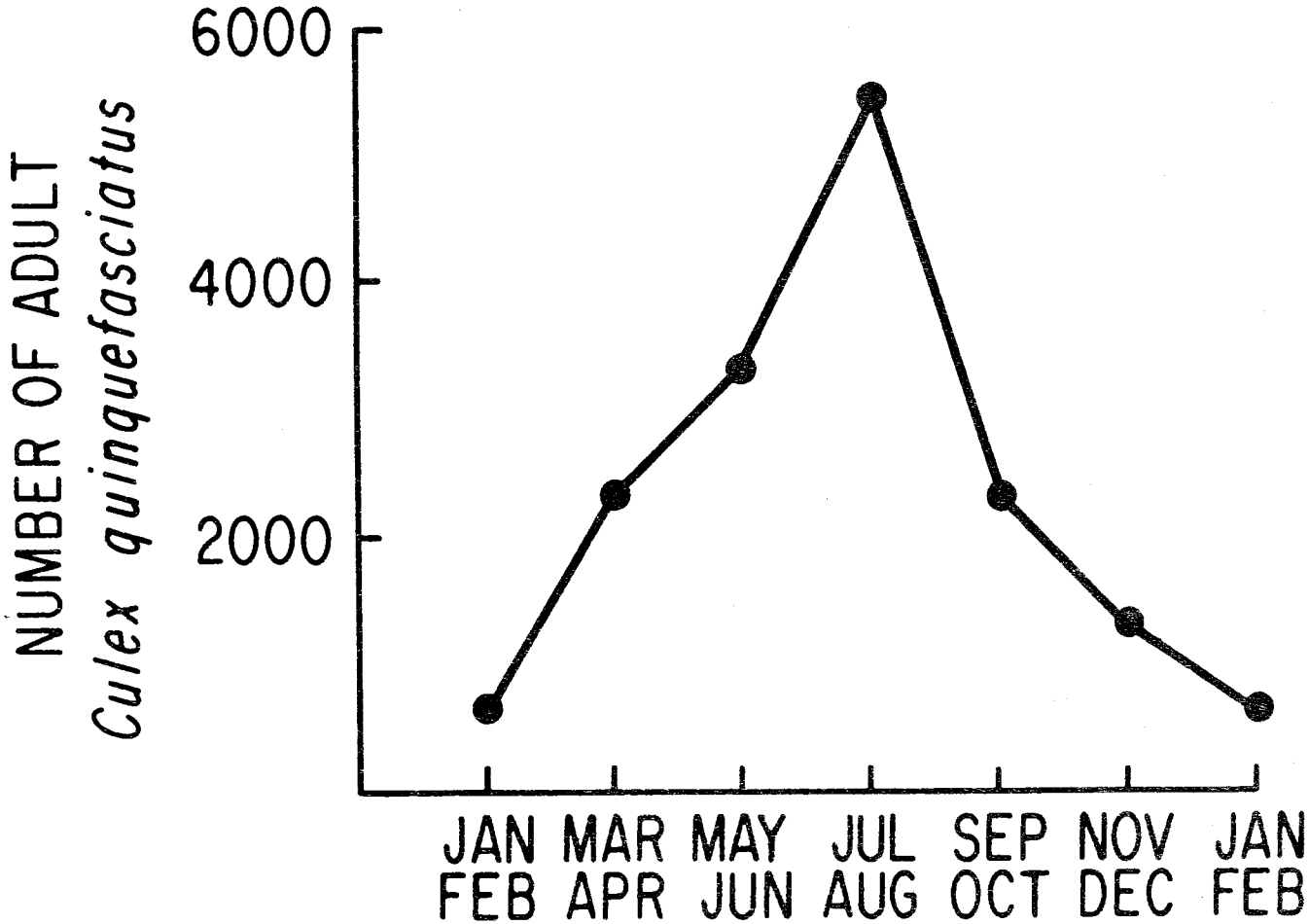


Figure 6. Maximum elevations at which mosquitoes were found on Mauna Loa throughout the yearly cycle.

Figure 7. Yearly Abundance of *Culex* (adult) on Island of Hawaii



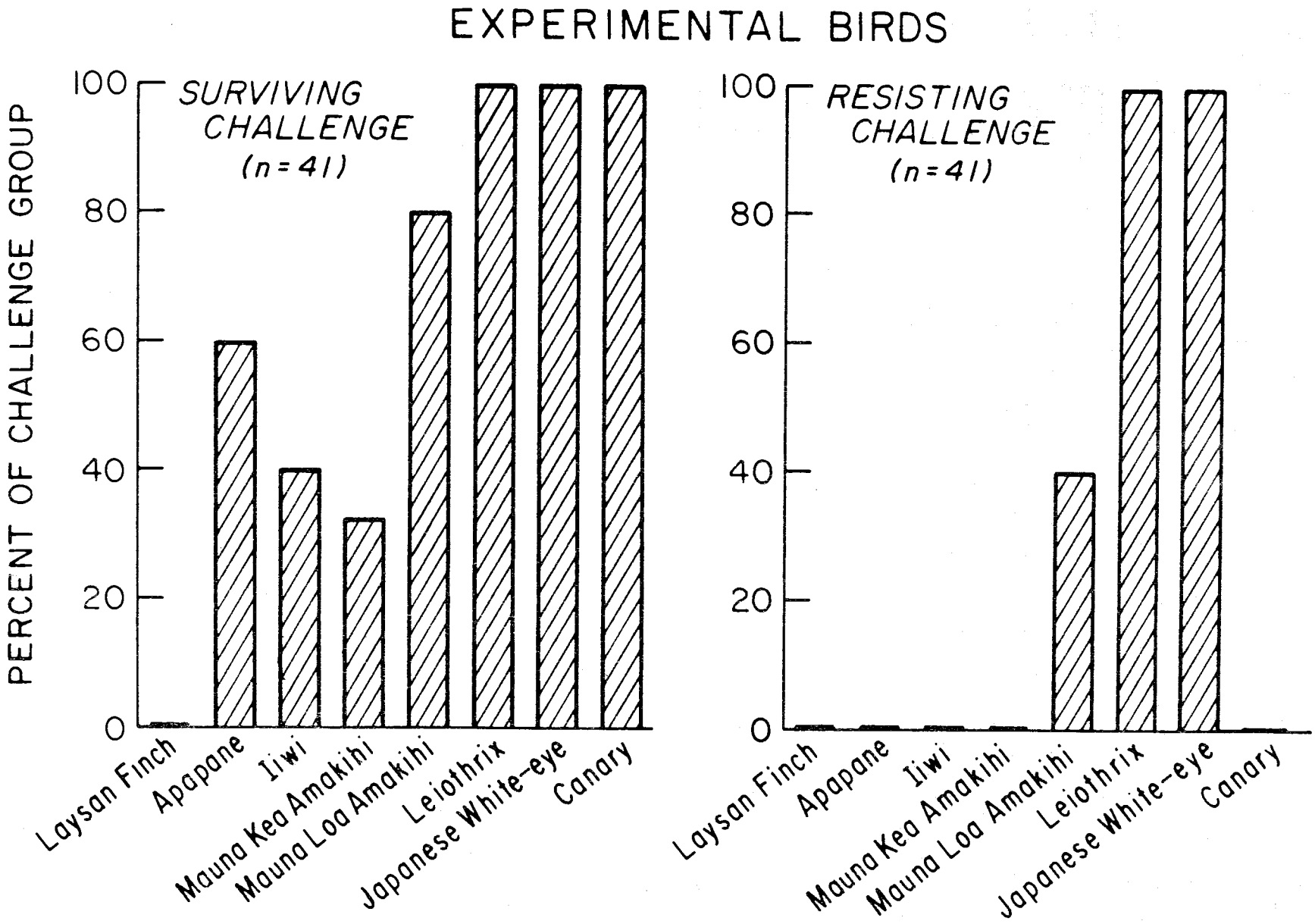


Figure 8. Percentage of individuals of challenged avian hosts resisting and surviving malaria challenge.

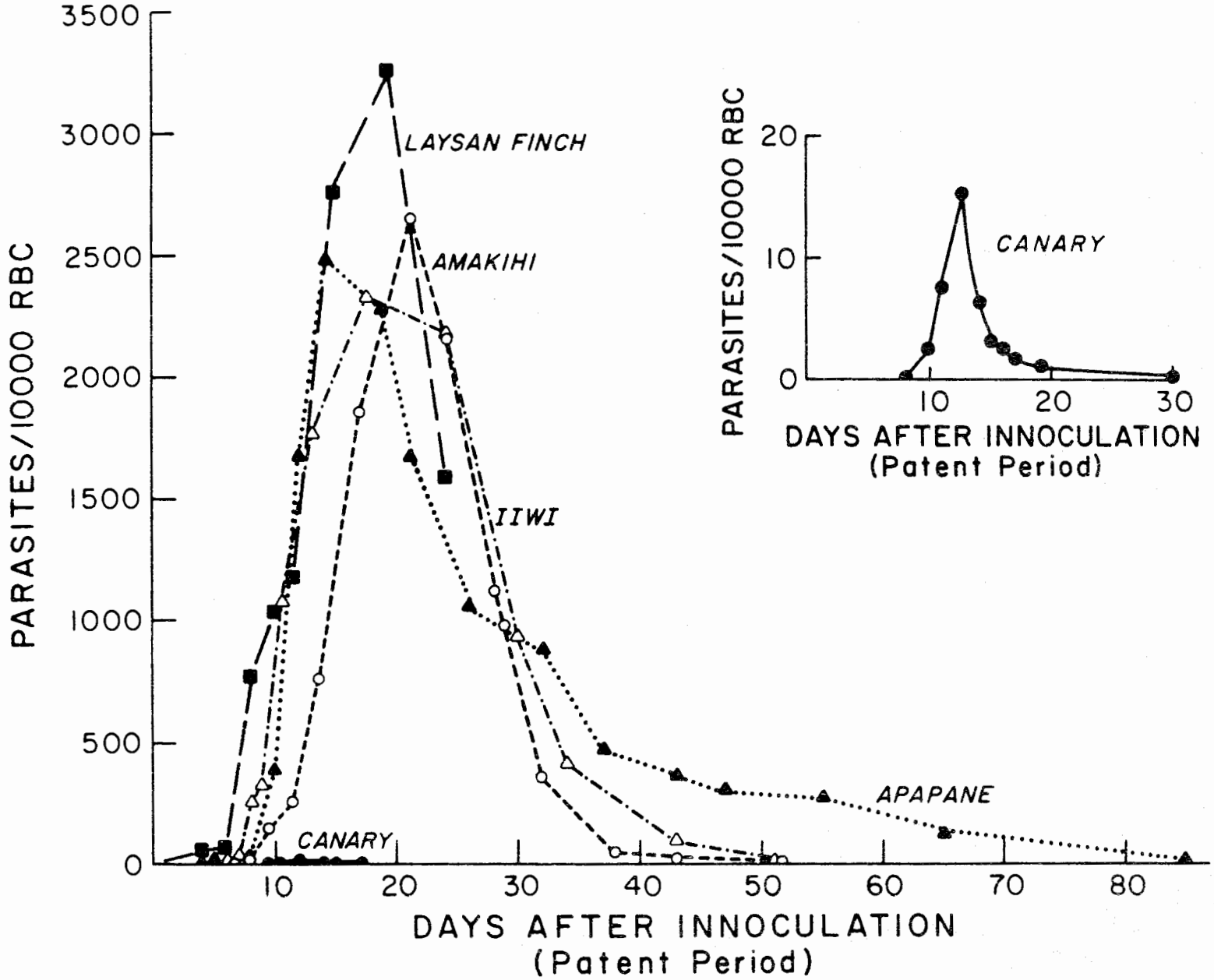


Figure 9. Parasite levels of avian hosts from Mauna Loa, Hawaii, over the patent period.

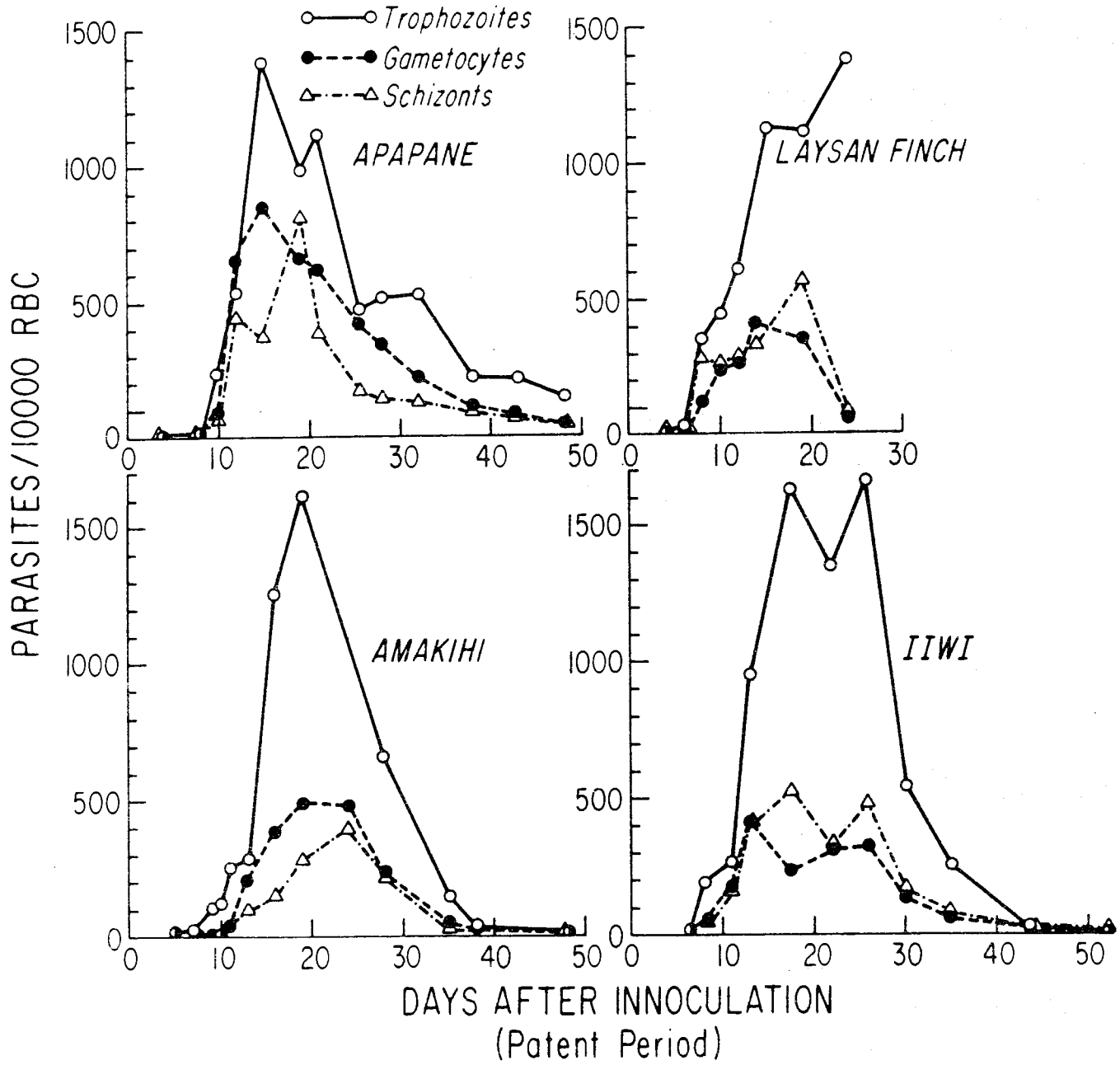


Figure 10. Numbers of trophozoites, gametocytes, and schizonts in challenged avian hosts from Mauna Loa, Hawaii.

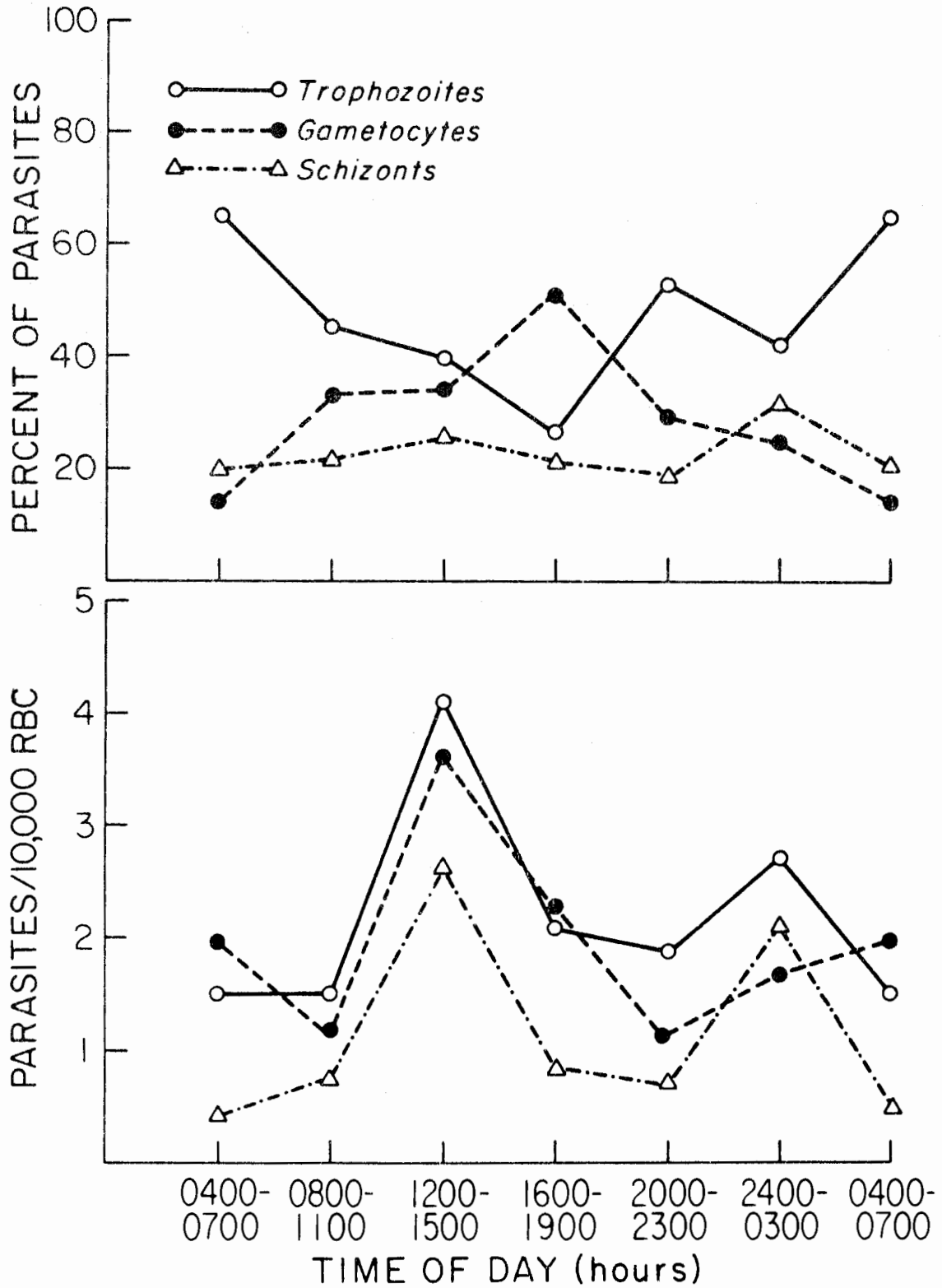


Figure 11. Parasite levels in avian hosts from Mauna Loa, Hawaii, over the 24 hour daily cycle.

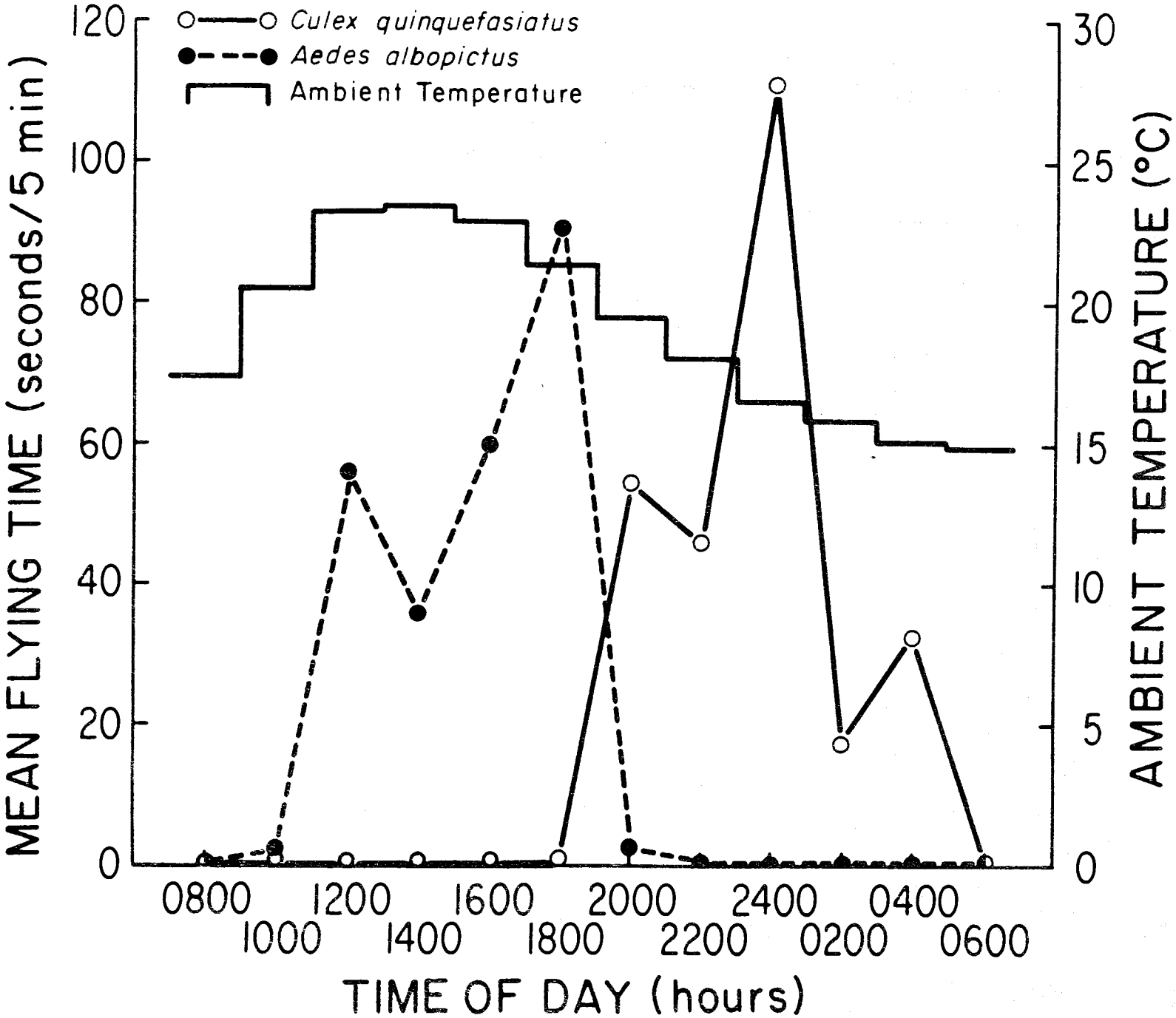


Figure 12. Daily activity levels of mosquitoes from Mauna Loa, Hawaii.

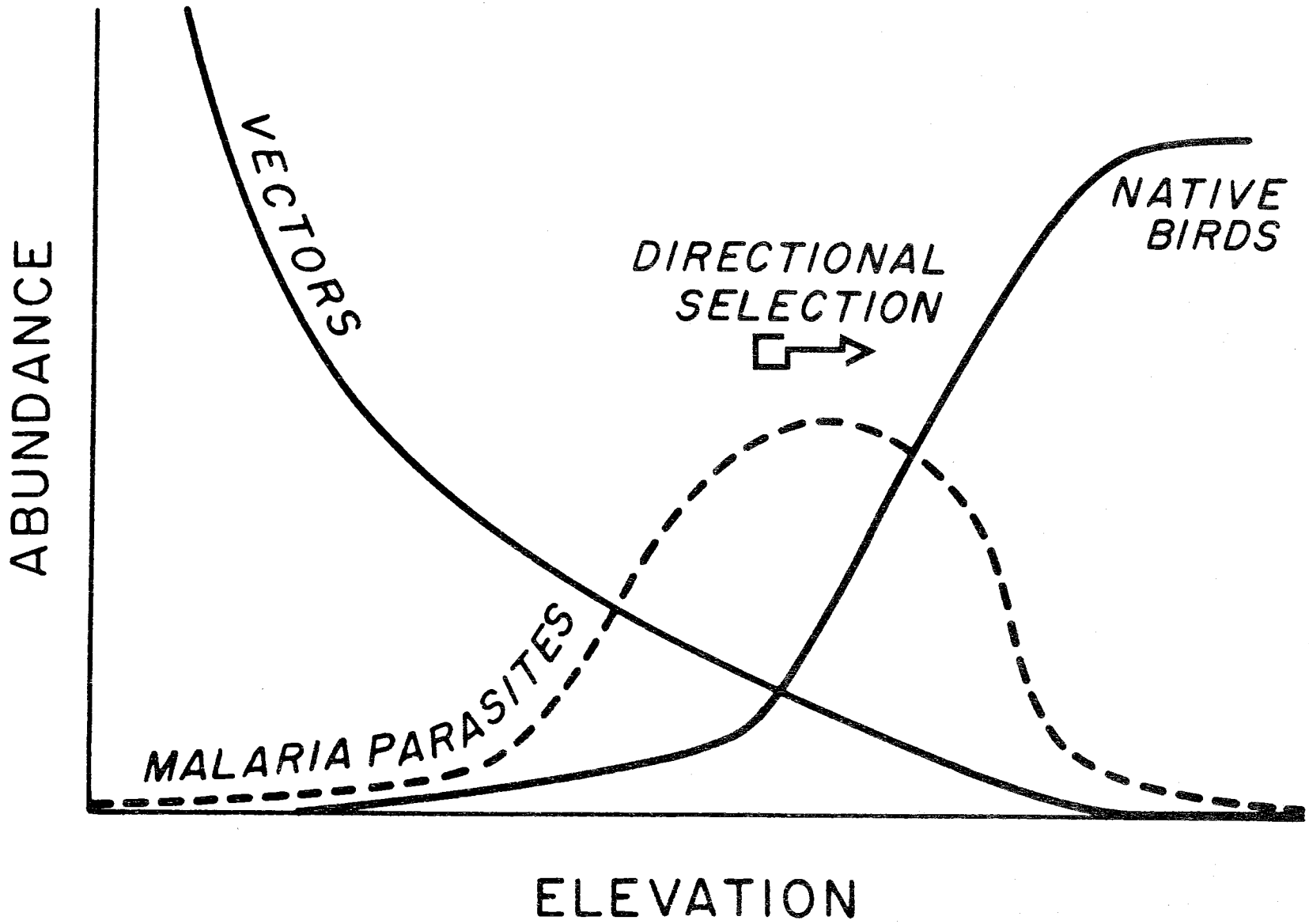


Figure 13. Native bird, malaria parasite, and vector abundances on Mauna Loa, Hawaii.

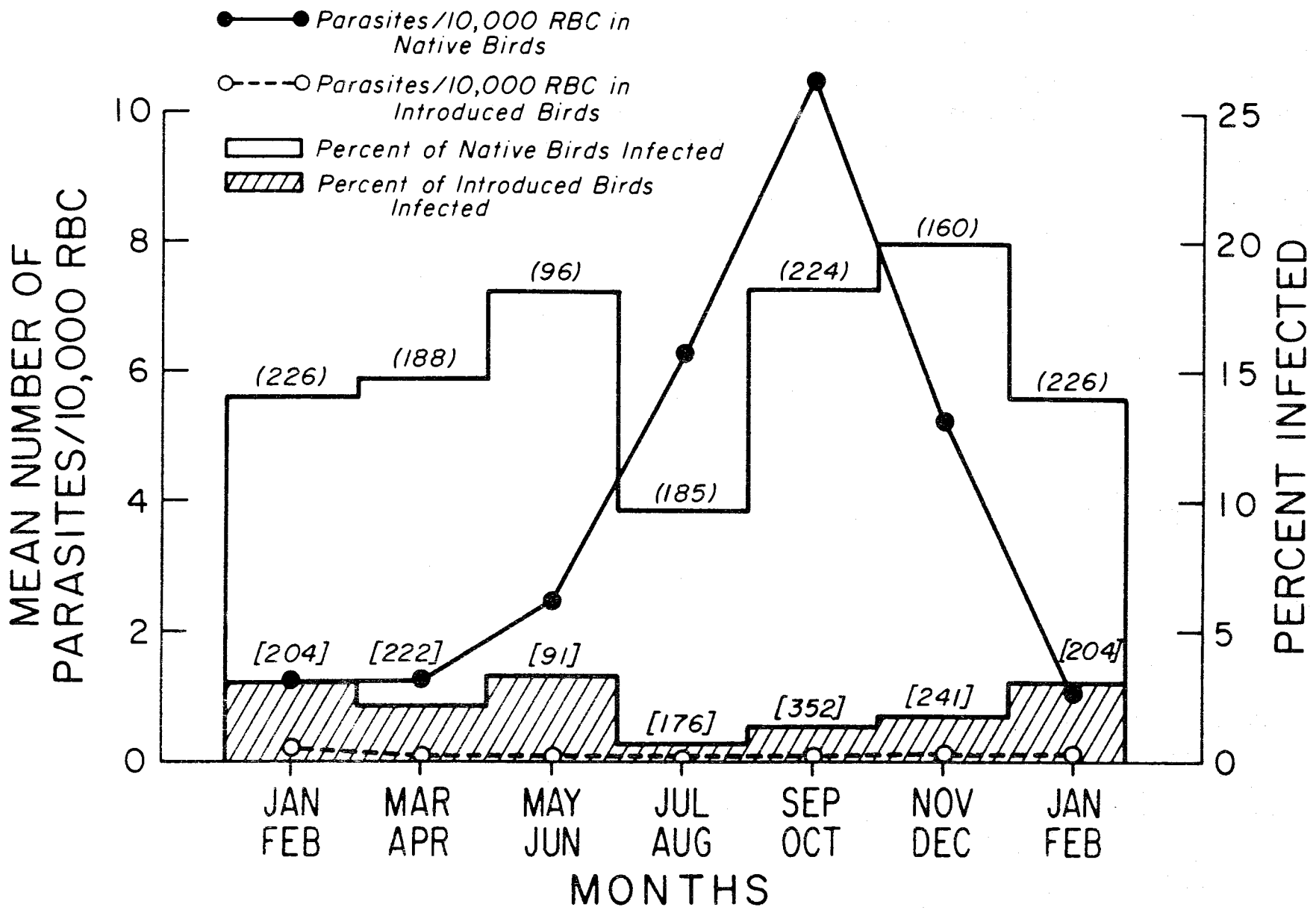


Figure 14. Introduced and native bird malaria parasite levels over the annual cycle on Mauna Loa, Hawaii.

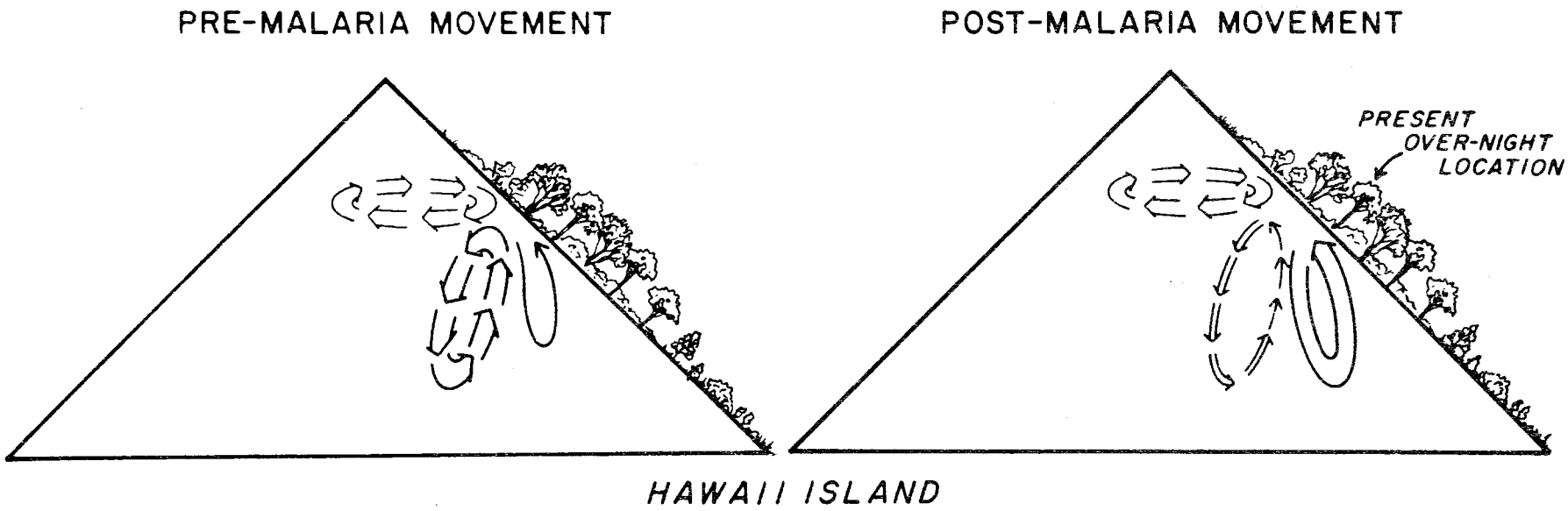


Figure 15. Pre- and post-malaria movement patterns of native Hawaiian birds on Mauna Loa, Hawaii.